88-04166/

Canadian Special Publication of Fisheries and Aquatic Sciences 100

Atlas of the biology and distribution of the squids *Illex illecebrosus* and *Loligo pealei* in the Northwest Atlantic

G.A.P. Black and T.W. Rowell

Department of Fisheries and Oceans
Scotia-Fundy Region
Biological Sciences Branch
P.O. Box 550
Halifax, Nova Scotia B3J 2S7

and E.G. Dawe

Department of Fisheries and Oceans
Newfoundland Region
Science Branch
P.O. Box 5667
St. John's, Newfoundland A1C 5X1

Department of Fisheries and Oceans
Ottawa 1987

© Minister of Supply and Services Canada 1987

Available from authorized bookstore agents, other bookstores or you may send your prepaid order to the Canadian Government Publishing Centre, Supply and Services Canada, Ottawa, Ontario K1A 0S9.

Make cheques or money orders payable in Canadian funds to the Receiver General for Canada.

A deposit copy of this publication is also available for reference in public libraries across Canada.

Cat. No. Fs 41-31/100E
ISBN 0-660-12774-1
ISSN 0706-6481

DFO/4048

Price subject to change without notice

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted by any means, electronic, mechanical, photocopying, recording or otherwise, without the prior written permission of the Publishing Services, Canadian Government Publishing Centre, Ottawa, Canada K1A 0S9.

A/Director: John Camp
Editorial and Publishing Services: Gerald J. Neville
Cover Design: Diane J. Dufour
Photo Credit: Bob Semple

Correct citation for this publication:

Black, G. A. P., T. W. Rowell and E. G. Dawe. 1987. Atlas of the biology and distribution of the squids *Illex illecebrosus* and *Loligo pealei* in the Northwest Atlantic, Can. Spec. Publ. Fish. Aquat. Sci. 100: 62p.

Contents

List of Tables iv

List of Figures iv

Abstract/Résumé v

Preface vi

Introduction 1

Data Presentation 1

Classification 2

Biology 3

- Life History Synopsis 3
- Distribution 3
- Interactions with Other Species 4
- Growth 4
- Reproduction 5
  - Maturity 5
  - Fecundity and Spawning 5
  - Early Life Stages 6
- Physiology 6

Fishery 7

- History 7
- Trends 7
- Catches 7
- Regulations 8
- Utilization 8

Future Prospects 8

- Short Term 8
- Long Term 9

Acknowledgments 9

References 59

List of Tables

1. Progression of the feeding pattern of *Illex illecebrosus* and *Loligo pealei*. 10

2. Northwest Atlantic fish predators of squid (*Illex illecebrosus* or *Loligo pealei*). 10

3. Nominal catches (tons) of short-finned squid (*Illex illecebrosus*) in the Northwest Atlantic from 1963 to 1985. 11

List of Figures

1. Drawings of *Illex illecebrosus* and *Loligo pealei*. 2

2. Map of NAFO Subareas and Divisions. 12

3. Hypothetical migration path of *Illex illecebrosus* off the Northeastern U.S.A. 13

4. Interannual distribution patterns of *Illex illecebrosus* off the Northeastern U.S.A. 14

5. Interannual distribution patterns of *Loligo pealei* off Eastern Canada. 15

6. Interannual distribution patterns of *Illex illecebrosus*. 16

7. Seasonal distribution patterns of *Illex illecebrosus*. 18

8. Seasonal distribution patterns of *Loligo pealei*. 22

9. Monthly distribution patterns of *Illex illecebrosus*. 26

10. Monthly distribution patterns of *Loligo pealei*. 28

11. Distribution patterns of *Illex illecebrosus* in relation to bottom temperature. 29

12. Distribution patterns of *Loligo pealei* in relation to bottom temperature. 32

13. Distribution patterns of *Illex illecebrosus* in relation to maturity stage. 34

14. Nominal world catches of squid. and all fish, and shellfish in marine and freshwater. 40

15. Nominal Canadian catches of squid in the Northwest Atlantic. 40

16. Nominal catches of *Illex illecebrosus* in the Northwest Atlantic, and biomass estimates. 41

17. Interannual distribution patterns of nominal catches of squid from NAFO Subareas. 42

18. Monthly distribution patterns of *Illex illecebrosus* - International Observer Program sampling. 46

19. Management areas and boundaries relevant to squid fisheries. 58

Abstract

Black, G. A. P., T. W. Rowell, and E. G. Dawe. 1987. Atlas of the biology and distribution of the squids *Illex illecebrosus* and *Loligo pealei* in the Northwest Atlantic. Can. Spec. Publ. Fish. Aquat. Sci. 100: 62 p.

The biology, distribution, and fisheries of the short-finned squid (*Illex illecebrosus*) and the long-finned squid (*Loligo pealei*) in the Northwest Atlantic are summarized for the Northwest Atlantic Fisheries Organization Convention area. The primary synopses are presented graphically (using maps and charts) as a visual representation of distributional patterns, and fisheries statistics. In consequence of its importance within the Canadian Fisheries Conservation Zone, greatest emphasis has been given to description of the short-finned squid and its fishery.

Résumé

Black, G. A. P., T. W. Rowell, and E. G. Dawe. 1987. Atlas of the biology and distribution of the squids *Illex illecebrosus* and *Loligo pealei* in the Northwest Atlantic. Can. Spec. Publ. Fish. Aquat. Sci. 100: 62 p.

L'article résume sommairement la biologie, la distribution et la pêche de l'encornet (*Illex illecebrosus*) et du calmar (*Loligo pealei*) à l'intérieur des zones de pêches de l'Organisation des Pêches de l'Atlantique Nord-ouest. On a utilisé une présentation graphique par cartes et diagrammes pour illustrer les principaux sommaires des patrons de distribution et des statistiques de pêche. À cause de son importance à l'intérieur de la Zone Canadienne de Conservation des Pêches, nous avons accordé une attention spéciale à l'encornet et à sa pêche.

Preface

Over the years, the Biological Sciences Branch and its several predecessors have collected vast amounts of resource information in order to gain an understanding of the state of the biological resources and the factors which influence their abundance and well-being. This information exists in various forms from handwritten reports in filing cabinets, to sophisticated, but unpublished data bases, through to assorted published reports on one or another aspect. Unfortunately, not enough is available in readily understandable and comprehensive form suitable for use by the fishing industry, the general public and our own Department.

In an attempt to improve on this situation, the Biological Sciences Branch has undertaken a program to display, in graphic form, resource information presented with relevant but deliberately spare supporting text. The ultimate intention, or goal, is to make available as much as is feasible of our accumulated information through production of a series of resource atlases. To accomplish this, a position of Fisheries Analyst was created with the incumbent working with scientists within the Branch and elsewhere, to seek out and assemble the data, followed by analysis, interpretation and the choice of the most appropriate means of display.

Since conveying resource information graphically has not yet reached the status of a science, the first incumbent, Mr. G.A.P. Black, has been faced with a development task of considerable and daunting proportions. Many tools are available with many different ways of analyzing and representing the data; major adaptations and further development were required to fulfill our intentions. Additionally, although many atlases displaying resource information are extremely beautiful examples of the cartographers' craft, not all are supported by data prepared with sufficient rigour to make them reliable; viewers can be seduced by the beauty of the presentation and not be aware of or overlook the shallowness of the data. To avoid this trap, we decided at the outset that in this series of atlases, the emphasis should be placed on objectivity, quantitative representations, comprehensiveness, simplicity and reliability, as well as good looks. To this end, Mr. Black has spent much time in assembling the data and developing the computer programs for analysis, and determining the best way to present the data, as well as to store it electronically in a form which permits ready access and updating.

We chose the squids, *Illex illecebrosus* and *Loligo pealei*, as the species to serve as guinea pigs in developing the art and to determine the extent to which we could fulfill the objectives stated above. It is my belief that Mr. Black has been successful in devising a system which meets these objectives. In the course of preparing this atlas and the sequel on the scallop, *Placopecten magellanicus*, he has together with the co-authors illustrated very well how this system functions in presenting resource information graphically. The two atlases, one on squids and the other on scallops, bring to a close the strictly experimental phase in which the foundation for the steady production of a continuing series of resource atlases has been laid.

James E. Stewart
Director
Biological Sciences Branch
Scotia-Fundy Region

Introduction

Canadians have been fishing for squids since the late 1800s and, since the development of a significant offshore fishery in the early to mid-1970s, have actively participated in the management of this valuable renewable resource. At its peak in 1979, the Canadian squid fishery was significant in relation to other Canadian fisheries, and to the international squid fisheries market. In consequence, a coordinated international research effort was initiated in 1980 under the aegis of the Northwest Atlantic Fisheries Organization (NAFO) to provide the biological information for an effective management regime.

By virtue of their geographic distribution, most squids caught in Canadian waters are short-finned squid (*Illex illecebrosus*), which form the major component of the squid fisheries and, for which the majority of the research data is available. Although long-finned squid (*Loligo pealei*) is regularly seen over the more western areas of the Scotian Shelf, only rarely are significant numbers present.

Specific critical aspects of the life cycle of *I. illecebrosus* remain to be confirmed by observation. The location of spawning is still unknown, although there is evidence that the major spawning areas are south of Cape Hatteras and probably in the Gulf Stream Frontal Zone over the Blake Plateau. Limited evidence also suggests that the species is passively and (or) actively migratory over long distances (Florida to Newfoundland and return). These factors, coupled with the extreme recruitment variability and unknown predator/prey impacts, argue strongly for fuller study and careful international management.

Included in this report is information on: the biology of both *I. illecebrosus* and *L. pealei*; the distribution of *I. illecebrosus* and the northerly extent of the distribution of *L. pealei*; the spatial distribution of *I. illecebrosus* in relation to the abiotic factors, time of year and sea-bottom temperature; and variation in these distributions in relation to the maturation of both males and females throughout their lifespan. Additionally, world squid catches are compared to world catches of all fish and shellfish species; squid catches, by statistical unit areas are tabled and mapped for recent years; and the spatial relationship between squid directed catch and bycatch are mapped on a monthly basis for a number of years.

This report is intended to provide a concise yet scientifically rigorous textual and visual synopsis of the biological and fisheries information available for *I. illecebrosus* and *L. pealei* in the Northwest Atlantic, concentrating on the Canadian fishing region. The report has been prepared for use by the industry, fisheries managers, and interested lay readers.

For a more detailed review of the biology of *I. illecebrosus* and *L. pealei*, the reader is also referred to O'Dor (1983) and Summers (1971), respectively. Note that unless otherwise specified, *Illex* refers to *Illex illecebrosus* and *Loligo* refers to *Loligo pealei*.

Data Presentation

Figures showing the spatial relationship of squids to relevant biological and abiotic parameters are presented in accordance with the guidelines of Bertin (1981). The maps are presented at small scale (using a Mercator projection) in *groups*, intending to convey a *graphic* representation rather than a cartographic product, emphasizing contrasts or similarities.

The choice of a presentation format involved the weighing of contradictory objectives, including: clarity, simplicity, resolution, precision, and uniformity. Two mechanisms were used to balance these objectives: discrete data scaling, and definition of the sampling area.

The data values used in developing the figures are discretely scaled using logarithmic transformations to provide a constant ratio of circle (symbol) size. The scaling varies between figures so as to minimize secant (overlapping) circles as much as possible. In the legend, the numbers bracketing a given circle, are the data group limits within which all data values are represented by the same sized circle.

On the maps, the area of sampling is indicated by an underlying grey shading. This defines the spatial area within which all sampling occurred for the given criteria and, as such, any extrapolation of squid abundance or variability outside these areas is hypothetical.

The data for a number of the figures were obtained from research surveys directed towards both the assessment of squid and groundfish stocks, using bottom trawl random stratified surveys. The results are presented as kg per tow, or number of squid per tow (1.75 nautical miles or approximately 30 minutes). While the variation in the effective catch-rate of the gear between the vessels cannot be eliminated, at the scale used in these figures, the data presentation is not significantly altered by this variation in sampling methods.

In order that the figures be comprehensible, much detailed information had to be aggregated. In most cases this was done using more than one parameter (e.g. time and geographic area). The reader is cautioned to consider that while these computer-generated maps are based on actual data, they do not represent absolute limits on the real spatial distribution and biological variability of the species.

Classification

Common Name:	Short-finned squid[1]		Long-finned squid	
Class:		Cephalopoda	Cuvier,1798	
Subclass:		Coleoidea	Bather,1888	
Order:		Teuthoidea	Naef,1916	
Suborder:	Oegopsida	d'Orbigny, 1845	Myopsida	d'Orbigny, 1845
Family:	Ommastrephidae	Steenstrup, 1857	Loliginidae	Steenstrup, 1861
Subfamily:	Illicinae	Posselt, 1890		
Genus:	*Illex*	Steenstrup, 1880	*Loligo*	Steenstrup, 1880
Species:	*illecebrosus*	(LeSueur, 1821)	*pealei*	LeSueur, 1821

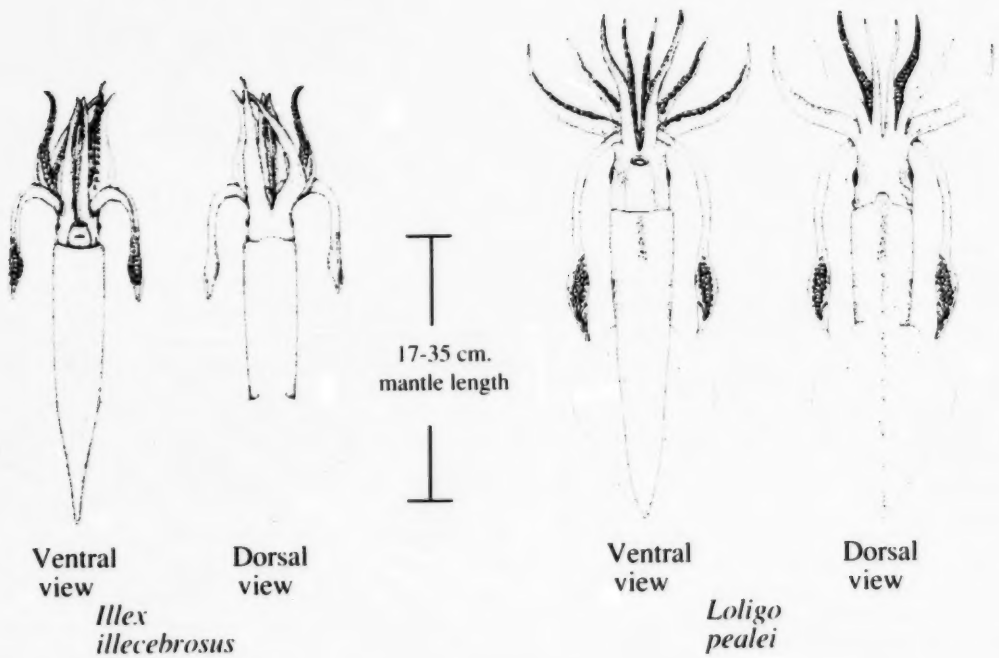


Figure 1. General representation of the dorsal and ventral view of *Illex illecebrosus* and *Loligo pealei* as adults (adapted from Roper et al., 1984). Note that although the scale is approximate, *Loligo pealei* are larger as adults.

[1] The English word "squid" is a dialectal variant of "squirt" and refers to the activity of the siphon during movement.

Biology

Life History Synopsis

There are four closely related species of *Illex* in the western Atlantic: *Illex illecebrosus*, *I. oxygonius*, *I. coindetii*, and *I. argentinus*, whose morphological similarity make species separation of adults difficult and, at present, impossible for larval and juvenile stages (Roper et al., 1969). *Illex oxygonius*, the sharptail shortfin squid, occurs in the western Atlantic from Chesapeake Bay to southern Florida and the southeastern Gulf of Mexico and in the eastern Atlantic in the Gulf of Guinea (Roper et al., 1984). *Illex coindetii*, the broadtail shortfin squid, occurs in the western Atlantic from southeast Florida throughout the Gulf of Mexico and Caribbean Sea and in the eastern Atlantic from Norway to the Gulf of Guinea including the Mediterranean and Black Sea (Roper et al., 1984). *Illex argentinus*, the Argentine shortfin squid, is found in the western Atlantic along the coast of Argentina and around the Falkland Islands (Hatanaka et al., 1985).

Illex illecebrosus is a pelagic cephalopod with an apparent life span of about 1-1.5 years. Spawning is believed to occur only once and the spawned animals probably die shortly after. The current hypothesis is that most of the population spawns south of Cape Hatteras, over the Blake Plateau, in late autumn and early winter (in water masses having characteristics midway between Continental Edge and Yucatan Straits Water) (Rowell et al., 1985*a*; Rowell and Trites, 1985). The egg masses are believed to be neutrally buoyant when released, and are transported north by the Gulf Stream (Rowell et al., 1985*a*; O'Dor and Balch, 1985). The distribution is related to water masses and temperature regimes. Adults are observed over the continental shelf from the southeastern U.S. to Newfoundland and Labrador during the summer and autumn. During autumn the maturing adults migrate southward to the spawning areas.

Loligo pealei, the second but much less important species in terms of relevance to Canadian fisheries, is related to two other loliginids of commercial interest in the western Atlantic, *Loligo* (*Doryteuthis*) *plei* and *Lolliguncula brevis*.[2] *Loligo* (*Doryteuthis*) *plei*, the arrow squid, occurs predominantly south of Cape Hatteras, in the Gulf of Mexico, and apparently as far south as northern Argentina. *Lolliguncula brevis*, the brief squid, occurs in coastal and estuarine waters, and has been observed from Maryland to Rio de la Plata, Brazil (Voss, 1956).

Loligo pealei is a pelagic cephalopod distributed from Canadian waters to the upper Gulf of Mexico and Cuba. *Loligo pealei* is generally found in very low abundance on the Scotian Shelf and then only on the the more western areas and in the Bay of Fundy (Rowell, 1986). Spawning occurs during the late spring and summer south of Cape Cod. *Loligo* has a life span of 1-2 years. Adults are found predominantly from Cape Hatteras to Nantucket Shoals.

[2] All are members of the family Loliginidae.

Distribution

The NAFO Subareas and Divisions are shown in **Figure 2** (*page 12*). The life cycle of *Illex* is generally understood with exception of the exact location(s) of spawning (**Figure 3**, *page 13*). Evidence suggests that the major spawning event occurs south of Cape Hatteras during December through January in the Gulf Stream/Slope Water frontal zone (Rowell et al., 1985*a*; Rowell and Trites, 1985). Secondary and tertiary spawning events occur in spring and summer and in some years are important contributors to the resource biomass in the more southern shelf areas (NAFO Subareas 5&6). Neutrally buoyant egg masses apparently drift passively in the subsurface region of maximum salinity of the Gulf Stream (O'Dor and Balch, 1985; Rowell and Trites, 1985). Hatching occurs in about 9-16 days (O'Dor et al., 1982). The resultant larvae and juveniles apparently continue to drift northward with the Gulf Stream and during the summer the juvenile *Illex* move onto the Shelf and into shallow water off northern New England, Nova Scotia and Newfoundland. On the Shelf, males undergo earlier maturation than females and appear, based on sex ratios, to migrate south during the fall in advance of the females (Lange and Sissenwine, 1983). Fully mature females have only rarely been encountered (Dawe and Drew, 1981). Evidence for a long-distance spawning migration includes tagging data for a squid released in Newfoundland and reported captured off Maryland, covering 2,027 km in 107 days (Dawe et al., 1981*a*).

Loligo spawn in the spring through summer in shallow water, primarily between Cape Cod and Cape Hatteras (Lange and Sissenwine, 1983). *Loligo* pr duced from the early spawning period may mature early and spawn during the late summer of the following year, otherwise they spawn during the spring and summer of their second year, with some surviving and spawning at about two years of age. They overwinter in deeper waters along the Shelf-edge.

Both species are distributed as far south as Florida; *Loligo* is also found in the northern Gulf of Mexico, although both species appear to be most abundant north of Cape Hatteras (Voss and Brakoniecki, 1985; Whitaker, 1980). The more northerly distribution of *Illex*, relative to *Loligo*, in the Georges Bank - Gulf of Maine area, is evident from the USA bottom trawl surveys (**Figure 4 & 5**, *pages 14-15*) (Whitaker, 1980), and the combined U.S.A. and Canadian bottom trawl surveys (**Figure 6**, *pages 16-17*). The general seasonal distribution of *Illex* north of Cape Hatteras is hinted at by the distribution of catches from the combined bottom trawl surveys of the Northeast Fisheries Center (USA), and Scotia-Fundy, Gulf, and Newfoundland Regions (Canada) (**Figure 7**, *pages 18-21*). The pattern of a northerly extension of range during summer and fall is also evident for *Loligo* (**Figure 8**, *pages 22-25*). For both species, especially *Illex*, a seasonal increase in abundance is evident. Although the catch rates between the regions and research vessels are not standardized, the overall pattern is clear. Seasonal

catches by bottom trawl research surveys vary from year to year. Aggregated monthly plots from 1970 to 1980 bottom trawl surveys indicate a general movement of *Illex* onshore and northward during the summer and a retreat southward during the fall (**Figure 9**, *pages 26-27*), and a similar monthly distribution of *Loligo* for the northeastern U.S.A. (**Figure 10**, *page 28*).

The onshore movement of squid to the Shelf areas takes place during spring and early summer when water temperatures are increasing, and there is evidence that distribution is influenced by bottom-water temperature (Scott, 1978). The detailed distribution of squid catches in relation to the bottom-water temperature from research trawl surveys suggests, however, that more than temperature influences the distribution of *Illex* (**Figure 11**, *pages 29-31*) and *Loligo* (**Figure 12**, *pages 32-33*). Bottom trawl research surveys during July 1970-1980 did not demonstrate a relationship between depth or bottom-water temperature and mean catch rate (Mohn, 1981); however examination of squid distribution patterns during 1980-83 indicated the highest concentrations on the Scotian Shelf were in the western area where bottom-water temperature exceeded 6°C. Despite this, high concentrations of *Illex* are regularly found in areas of low bottom-water temperature, which appears to be a preference rather than a requirement (Rowell et al., 1985*b*). Migration inshore, to and over the continental shelf, appears linked to food availability.

Interactions with Other Species

The trophic relationships of *Illex* (Ennis and Collins, 1979) and *Loligo* (Vovk, 1974) are similar. The food of both species consists of primary, secondary, and tertiary consumers, while both are prey species, mainly at the fourth trophic level.

A Scotian Shelf study of the interactions of *Illex* with cod, haddock, pollock, silver hake, yellowtail flounder, red hake, redfish, and environmental factors (location, depth, salinity, surface and bottom-water temperature) indicated *Illex* (and silver hake) catch rates were simultaneously positively correlated with bottom-water temperature, salinity, sediment particle size, and depth (Waldron, 1983).

In the coastal waters of eastern Newfoundland and Labrador, a study of *Illex* predation on cod, capelin, and herring suggested a possible predation effect (significant negative correlation) between squid abundance and capelin (NAFO Div. 2 & 3K), assuming squid prey on age-group 0 and 1 capelin (Dawe et al., 1981*b*). Additionally, in Newfoundland inshore waters, cod have been found to be the most important fish prey on the northeast coast, with redfish the only fish prey species observed from south coast samples (Dawe et al, 1983). Fish were identified through otoliths found in the stomachs of the squid sampled. An increase in the incidence of cannibalism, as the season progressed, appeared to be related to a decrease in the availability of other prey species.

As both *Illex* and *Loligo* grow, the diet changes from one dominated by crustaceans to one composed largely of fish and squid (**Table 1**, *page 10*) (Amaratunga, 1983; Amaratunga et al., 1979; Froerman, 1984; Maurer and Bowman, 1985; Vinogradov, 1984; Vovk, 1983). *Illex illecebrosus*, obtained from groundfish surveys in the Gulf of Maine to the Cape Hatteras area during the spring, summer, and autumn of 1979-80 fed primarily on squid (56% of stomach contents by weight), while *Loligo* fed primarily on fish (56.2%) (Maurer and Bowman, 1985). Scotian Shelf sampling of *Illex* indicates that feeding frequency is reduced as the season progresses (Amaratunga et al., 1979).

Illex was found to be the almost exclusive diet of the long-finned pilot whale (*Globicephala melaena*) in Newfoundland waters, with the two arriving and departing the region annually, almost simultaneously (Mercer, 1975). A population of 50,000 pilot whales was estimated to consume 166,000—249,000 tonnes during 100 days of residency in inshore Newfoundland waters.

Fish predators of *Illex* and *Loligo* (**Table 2**, *page 10*) include common demersal species such as cod, haddock, pollock, red and silver hakes and many others (Lange, 1980). In years of high abundance, *Illex* was a common prey item for cod (especially larger cod) around Newfoundland, although not as significant as either capelin or sand lance (Lilly and Osborne, 1984).

Growth

Estimates of the growth rate of *Illex* vary considerably. Growth estimates from size data are affected by immigration and emigration within the sampling region. Squid sampled from Newfoundland catches between May and October doubled in mantle length and exhibited an average 6-fold weight increase over the 5 month period (a 1.0-4.0 cm. increase in mantle length/month) (Squires, 1957). Mesnil (1977) reported growth rates of 1.6 cm/month for males and 1.9 cm/month for females. Von Bertalanffy growth curves indicate sexual, areal, and interannual variability in growth (Amaratunga, 1980).

Feeding studies indicate a food conversion efficiency of 35%-51% (O'Dor et al., 1979). Refined measures of average daily feeding rate (5.2% of body weight), average daily growth rate (1.3%), and average daily feeding rate for maintenance (1.8%) have been reported, where the daily feeding rate varied from 0%-15% of body weight apparently due to behavioural interaction in the school (Hirtle et al., 1981). Additionally, assimilation efficiency has been estimated at 0.86 (Wallace et al., 1981).

Loligo growth has been estimated at 1.7-2.0 cm/month during the summer period, ranging to 0.4-0.6 cm/month over the winter (Mesnil, 1977). Growth estimates of *Loligo* from the Gulf of Mexico were similar to those from northern areas (Hixon et al., 1981).

Reproduction

Maturity

A consensus is lacking as to which of the several maturity-stage scales used is most valid in representing the progression of maturation in *Illex* and *Loligo pealei*. (Juanico, 1983). Different maturity-stage indices are used for each sex. Among the various scales, that for *Illex* females is relatively objective, being based on the ratio of nidamental gland length (NGL) versus mantle length (ML) (Durward et al., 1979). NGL/ML ratios have been found to correspond reasonably well with the histological condition of the ovaries (Coelho et al., 1982). The scale for males is subjective, and there is little doubt that its application by various investigators may be inconsistent (Mercer, 1973*a*; Durward et al., 1979; Amaratunga and Durward, 1979).

The apparent earlier maturation of the male *Illex* may be the artifact of a truncated male maturity index scale. As spermatogenesis is apparently continuous from an early developmental stage, three other reproductive features have been suggested as maturation indicators; spermatophore morphology (Voss, 1983), spermatophore number (O'Dor et al., 1980), and degree of hectocotylization (Schuldt, 1979). Samples of *Illex* from St. Margaret's Bay (Nova Scotia), Newfoundland, and a captive population (Dalhousie University) suggest that relative hectocotylization is an unreliable index of maturity, but may be an indicator of environmental conditions experienced during development (Coelho and O'Dor, 1984). Accidental loss of spermatophores may invalidate spermatophore counts as an adequate index. A preliminary maturity-stage index comprising 9 stages based on reproductive/ecological scales has been proposed to provide further differentiation (Burukovsky et al., 1984).

Bottom trawl surveys of *Illex* on the Scotian Shelf between 1979 and 1983 indicated differences in the monthly and spatial distribution of maturity stages (**Figure 13**, *page 34-39*). Analysis of these data for the 1980-83 period indicated that maturation varied from year to year, and may be associated with the considerable variation in between-year and within-year size distributions. Length frequencies showed a general increase in modal length of the primary cohort from July to September, with secondary and tertiary cohorts of smaller *Illex* in the western regions of the Shelf during September and October being relatively more abundant in low biomass years (Rowell et al., 1985*b*). Growth curves for 1977-1979 showed general yearly similarities, with the males maturing earlier and at smaller mean length than females (Amaratunga, 1980).

Only seven female *Illex* in advanced stages of maturity are known to have been captured, all in the period 1968-1980 (Dawe and Drew, 1981). Captures were reasonably evenly spread from Cape Hatteras to Bay of Islands, Newfoundland and provide no indication of probable spawning area(s).

Fecundity and Spawning

Mating behavior of *Illex* has been neither fully observed or described, although the few brief episodes of courtship behavior observed between captive squid suggest a pattern similar to that seen in *Loligo* (see below) but possibly less pronounced or more secretive (O'Dor et al.,1980; O'Dor, 1983). Observation on fully mature captive males suggests they may accumulate several hundred spermatophores in advance of mating. Mating is triggered by the presence of fully mature females, and results in the implantation of male spermatophores in the female mantle cavity. Individual males may mate with more than one female (O'Dor et al., 1980). Mating may take place well before spawning. During the spawning of *Illex illecebrosus*, eggs from the oviducts, sperm from the implanted spermatophores, and jelly from the nidamental glands, are mixed with seawater and exuded slowly into a spherical gelatinous low density egg mass (O'Dor et al., 1980). The density of the egg mass is determined by the density of the eggs (with a specific gravity of 1.10), the gelling agent, and the constituent seawater. Because the bulk of the mass is seawater, the mass is almost neutrally buoyant and may become neutrally buoyant if the surrounding water increases in density (through a decrease in temperature or increase in salinity) as generally occurs with increasing depth in near-surface waters. The egg-mass buoyancy, rate of temperature equilibration, and terminal velocity affect the sinking rate. The ecological significance of this is that the spawning location (yet to be discovered), must provide a physical environment that results in a sinking rate such that the egg mass remains within a suitable temperature regime throughout the incubation period. Females may produce more than one egg mass, and still not be completely spawned out (eggs have been observed in the ovary of dead females after spawning) (Durward et al., 1980).

Egg masses obtained in laboratory spawnings contained up to 100,000 ova, spaced about 1-2 cm apart and were 0.5-1.0 m in diameter (Durward et al., 1980; O'Dor and Balch, 1985). Although egg counts indicate a potential of about 5×10^5 ova per female, true or functional fecundity may be well below this, since fully mature males may, by the placement of their spermatophores, stimulate premature spawning in females (O'Dor et al., 1980). Less than half of the spawned eggs survived the incubation period under the laboratory conditions.

When *Loligo* are held in captivity, they usually school as a group. However when mating behaviour is induced, the males become increasingly excited, and begin darting about, challenging other males, and attempting to separate individual females from the school. A preference is shown for particular females. When a male is courting a female, a median arm is held upwards in an "S" shape, while the chromatophores in front of his eyes are expanded to form a dark brown patch. Challengers may displace males, resulting in the largest or strongest males coupling with the most desirable females. During copulation the male, flashing his chromatophores swims beside and slightly below the fe-

male. The male grasps the female with his arms around the mantle, and pulls himself forward so that his arms are close to the mantle opening. The male uses his hectocotylus (a modified arm) to reach inside his own mantle and pick up a bundle of spermatophores from the penis. The spermatophore bundle is then "cemented" to the inside of the females mantle or oviduct; the male releases the female. The entire process is consummated in 5-20 seconds. During spawning, the female produces a jelly-like egg capsule from the oviduct. The egg capsule is implanted with sperm released from the transferred spermatophores. The female takes the egg capsule in her arms so that the sticky end, containing no eggs; faces outwards. The egg capsule is commonly fastened to seaweeds such as *Fucus*, or if possible, attached to an existing egg mass, by pushing the sticky end of the egg capsule into the centre of the egg mass (Arnold et al., 1974).

Early Life Stages

As an aid in identifying and aging egg masses, a developmental staging scheme for in vitro and in situ spawned *Illex* was developed by O'Dor et al. (1982) based on previous work on *Illex coindetii* (Naef, 1923) and *Todarodes pacificus* (Hayashi, 1960). In their study, O'Dor et al. (1982) demonstrated that embryonic development failed at temperatures below 12.5°C, while the development rate at 21°C was nearly twice that at 12.5°C.

The larvae of *Illex* have been described as Rhynchoteuthion type C', on the basis of morphological differences between a small number of larvae sampled from Cape Hatteras to Georges Bank (Roper and Lu, 1978; Vecchione, 1978).[3] Subsequently, a large sample of juveniles between the Gulf Stream and the edge of the Canadian continental shelf indicated the Gulf Stream contributed to the distribution of the early life stages (Amaratunga et al., 1980; Fedulov and Froerman, 1980; Rowell et al., 1985*a*; Dawe and Beck, 1985*a*,*b*). Additionally, the occurrence of 0.8-1.0 mm larvae in the Gulf Stream at a latitude of 31.5° N, suggested that spawning probably occurs south of Cape Hatteras (Rowell and Trites, 1985; Trites and Rowell, 1985).[4]

Physiology

The respiration and swimming performance of *Illex* has been studied experimentally (Webber and O'Dor, 1985). *Illex* has a negative buoyancy of 3%-4%. While swimming (tail first), the body is angled upwards by the jet to maintain its position vertically, and the squid uses 6 times more energy than sockeye salmon per unit distance travelled for speeds of 1 and 2 body lengths/second. The rate of O_2 consumption increases exponentially with swimming speed resulting in a critical swimming speed of 1.6 - 2.2 body lengths/sec. (62-88 cm/sec.). The most economical speed of transport was estimated to be 50-70 cm/sec. The long-distance migration of a tagged *Illex* (see Distribution above) represented an average speed of at least 22 cm/sec.

Squids have proven to be useful experimental animals for investigating neurophysiology and vision. The giant axon found in squid is sufficiently large to permit dissection and facilitate the conduct of experiments in neurophysiology. The large and well developed eyes of squids indicate a high degree of dependence on or use of visual information. As a result, the physiology and biochemistry of vision generally have been studied using the eye and optic lobes of *Loligo* (Arnold et al., 1974). Squid behavior when attacking jigs (see below) and their apparently great ability in net avoidance (O'Dor, 1983) can be associated with a strong response to visual stimuli.

---

[3] Rhynchoteuthion was used to describe these larvae, referring to the fused tentacles forming a proboscis (*Rhynchos* - snout [Greek]). The proboscis later separates into distinct tentacles during the transitional stage. The final separation is used as the criterion for definition of the change from larval to juvenile stages.

[4] Rhynchoteuthion Type B' larvae (probably Ommastrephes) were found during the survey and overlap the distribution of Type C' (believed to be *Illex illecebrosus*). The spawning location cannot be inferred exactly as the larvae were being transported by the Gulf Stream at a maximum rate of about 120 km/day.

Fishery

History

Squid jigging (and trap fisheries to a lesser degree) for *Illex* developed off Newfoundland during the late 1800's (Hurley, 1980). Catches from these fisheries occur during the summer months, peaking in September, and historically were used primarily for bait in the longline cod fishery (Squires, 1957). Through the 1970's, markets for squid for human consumption in Japan, the Soviet Union and Spain expanded or opened up for *Illex* (Dawe, 1981). Squid jigging remains an important fishing method when squid are available inshore, particularly in Newfoundland (Mercer, 1973*b*). Squid jigging was initially conducted solely by hand from small inshore boats. The lure or jig is about 70 - 120 mm long and consists of one or more rings of sharp barbless hooks with an ellipsoid lure above (Hamabe et al., 1982).[5] The jig is rhythmically jerked upwards through the water to attract the squid and ensure that it remains on the hook. Automated squid jiggers are now used, especially on larger vessels, to permit the setting of a larger number of lines simultaneously.

Squid fishing in the U.S.A. (Maine to N. Carolina) began in the late 1800's as incidental catches of both *Illex* and *Loligo* in the summer otter trawl fisheries and the inshore Massachusetts trap fisheries. Catches were used as bait for cod fishing, to supply small fresh fish markets or, failing these uses, was discarded (Lange, 1980).

The Soviet distant-water fleet first reported squid catches as part of the trawl fishery in 1964, and the Japanese started reporting in 1967. The fishery began off the U.S.A. in the late 1960's and subsequently along the Scotian Shelf in the early to mid 1970's (Lange and Sissenwine, 1983). It is interesting to note that although the distant-water fleets also fish the Grand Banks, little of the Subarea 3 (Newfoundland) catch is taken offshore. Even in the peak year of 1979, the bulk of the fishing in Newfoundland was by inshore trap and jig. The reverse was true on the Scotian Shelf and off the U.S.A. where the greatest part of the fishery took place along the Shelf-edge. Bottom trawling, midwater trawling, and squid jigging have been used by the distant-water fleets. Bottom trawling is the most economically efficient, but, as the quality standards for processing squid are high, the larger catches made by trawlers may result in wastage when the entire catch can not be processed before it spoils (Wiseman, 1982). While squid jigging results in the best quality product, large offshore squid-jigging vessels may not be able to fish other species when, as in the northwest Atlantic, the season is short (Wiseman, 1982).

Trends

The 1960's saw an increase in the total world landings of all marine species, which leveled off after 1971. The annual increase in the world catch since 1970 has been 1%-2% (Worms, 1983).[6] Squid landings accounted for only about 1.5% of the world landings throughout the 1970's (**Figure 14**, *page 40*).

The size of world-wide commercially important squid stocks has been estimated as high as 49 million tonnes (Lipinski, 1977) in comparison to 1985 world landings of squids, cuttlefishes and octopuses of 1,672,033 tonnes (FAO yearbook, 1987).

Catches

Peak catches for NAFO Subareas 2, 3, 4, and 5+6 took-place in 1974, 1979, 1979, and 1976 respectively (**Figures 15-17**, *pages 40-45*). Catches vary by more than an order of magnitude and may be taken variously as an index of availability of squid in the fishing areas, as a reflection of varying market demand, and somewhat more tenuously, as a possible indicator of overall abundance. Research survey data show that the peak catches in Subareas 3 & 4 were indicative of greater abundance over these areas of the Shelf, but the declining U.S. catches in Subarea 5 & 6 after 1976 are not indicative of reduced abundance over those areas. Rather they reflect a management regime which restricts catch levels.

The great variation in catch results in a fishery, which in its poor years has little economic value, but in its best years (such as 1979) has been among the most valuable in Canada (comparable to scallops and lobsters when the value of the international market is considered). The International Observer Program of the Department of Fisheries and Oceans has sampled both domestic and foreign fishing fleets since 1979. Although observers are not able to sample all catches, the data are representative of the commercial fishery. The yearly variation in catches, and the geographically restricted directed fishing zone of Subarea 4 (the Small Mesh Gear Line) are shown in **Figure 18** (*pages 46-57*).

By-catches of *Illex* and *Loligo* by the distant-water fleets (primarily the U.S.S.R. and Poland) began to be reported in 1964, and became increasingly significant when fishing for silver hake, red hake, mackerel, and herring commenced and necessitated regulatory control (see below).

[5] The colour of the jig can apparently be determined by the squid at a distance of 3 metres at 5 metres depth. At night, the stem of the jig is visible at 1 metre, where attacking squid have been observed to pause momentarily, close to about 60 cm and then attack. While squid do not struggle noticeably as the jig is hauled in, an adequate rate of retrieval is required to prevent the squid from disentangling its arms from the hooks. Observation on large schools, indicates that the squid hold off until one individual makes an attack, which initiates simultaneous attacks by many others.

[6] The 1980 total world landings were over 72 million tons.

Regulations

Management and regulation of squid resources was initiated in 1974 by the International Commission for the Northwest Atlantic Fisheries (ICNAF).[7] Distant-water fishing fleets began reporting squid in 1964 (U.S.S.R., 4 t), and by 1973 reported catches totaling 45,090 t (Lange and Sissenwine, 1983). A preemptive quota set the total allowable catch (TAC) of *Loligo* (only) at 71,000 t for 1974. At that time the catch statistics did not separate *Illex* and *Loligo*, but the majority of the catches off the U.S.A. were of *Loligo*. The *Illex* fishery was just developing. In 1976, separate TACs were established in the northeastern U.S.A. (Subareas 5 & 6) of 30,000 t for *Illex*, and 44,000 t for *Loligo*. Subareas 2-4 were assigned *Illex* TACs of 15,000 t (Int. Comm. Northwest Atl. Fish. Redbook, 1975). Both *Illex* and *Loligo* were managed as single stocks throughout their distribution ranges. The extension of jurisdiction by Canada and the U.S.A. in 1977 resulted in the formation of 2 management regimes.

After the U.S.A. Fishery Conservation and Management Act became effective in 1977, the U.S.A. withdrew from ICNAF and assumed management responsibility for the fishery resources within 200 miles of its coast. The National Marine Fisheries Service (NMFS) and the South Atlantic, Mid-Atlantic, and New England Fishery Management Councils jointly developed a Fisheries Management Plan, which established the TACs for *Illex* and *Loligo* at 30,000 t and 44,000 t, respectively. 'Fishing windows'[8] were established to regulate the foreign squid fisheries in time and place (**Figure 19**, *page 58*). In the U.S.A., both *Illex* and *Loligo* are currently managed on an April 1-March 31 fishing year (Lange, 1984*a*; Lange, 1984*b*).

In 1977, Canada assumed management responsibility for the fisheries resources within a Fisheries Conservation Zone extending 200 miles off its coast. Canada first solicited advice from ICNAF (and subsequently NAFO) on the management of *Illex* in 1974. In 1977, the TAC in Subareas 3 & 4 was set at 25,000 t. For Subareas 4VWX, the bycatch of juvenile haddock associated with the silver hake fishery prompted the introduction in 1979, of the Small Mesh Bottom Trawl Fisheries Regulations, which provided for the use of codends under 130 mm inside a restricted zone extending seawards from the shelf-edge, from April 15 to November 15 (**Figure 19**, *page 58*). Subsequently, the fishing season was further restricted to a July 1 - November 15 period. A multispecies management regime for both *Illex* and silver hake is implemented through the enforcement of this regulation, in conjunction with TACs and bycatch restrictions for both species. In 1980, in response to previous catches in excess of the existing TACs, a TAC of 150,000 t was established to protect against fishing mortality above 40% in years of moderate abundance (Northwest Atl. Fish. Organ. Sci. Coun. Rep., 1980). The reduction in fishing effort in subsequent years suggests that the fishery is self-regulating in years of low abundance (Northwest Atl. Fish. Organ. Sci. Coun. Rep., 1984).

Utilization

Utilization of squid as bait has been important since the beginning of the Newfoundland fishery over a century ago. A small dried squid industry, with export for human consumption to China, existed in 1910 and lasted until 1948. This market was revived in 1978 (Hurley, 1980). The primary utilization of squid from the northwest Atlantic since 1976 has been for human consumption as whole, cleaned and slit (mantle), or as tubes (mantle) in a variety of forms — fresh, frozen, dried, semi-dried, or half-skinned (Wiseman, 1982).

Japan is the most important market for squid; an estimated 600,000 t are available for annual consumption in its domestic market (2.8 kg per capita) (Wiseman, 1982). Other markets include Spain, Hong Kong and eastern Europe; the Canadian market is tiny.

Future Prospects

Short Term

With catches of *Illex* varying by as much as a factor of 60 in individual years between 1969 and 1979 in NAFO Subareas 2-4 (**Table 3**, *page 10*), there is no prospect for a stable fishery. In contrast, the fishery in Subareas 5 & 6, while showing the same trends and fluctuations, is much more stable. The population dynamics of *Illex* are not yet well understood, thus the effects of increased fishing effort are not yet clearly separable from other factors which contribute to the fluctuations.

The apparent resilience of cephalopods to intensive fishing has been linked to their alternative life strategy (lower fecundity, reduced number of spawnings, larger eggs with presumably a lower mortality rate) in comparison to that of

[7] ICNAF was established in 1950 to promote the conservation and optimum utilization of the fishery resources of the Northwest Atlantic area within a framework of international cooperation by participating countries. The successor to ICNAF, NAFO was approved January 1, 1979 by Canada, Cuba, the E.E.C., G.D.R., Iceland, Norway and the U.S.S.R. based on a similiar objective of multilateral cooperation.

[8] 'Fishing windows' are areas along the northeastern USA, over the continental slope, designated for foreign fishing within specified fishing seasons.

longer-lived bony fish. Their relatively low fecundity may result in significant abrupt declines in stock size when the parent stock is overfished (Caddy, 1983). In the short term there is no prospect for predicting stock levels of *Illex* even a few months in advance of the fishery: the life span of the species is too short and knowledge of the biotic and abiotic factors influencing spawning success and survival of the early life stages (larvae and juveniles) is too rudimentary. In years of high abundance, the economic value of the species may be extremely high and the ecological impacts are likely to be highly significant to other fish stocks .

Catches of *Loligo* are likely to remain relatively unimportant in Canada's fisheries, although in certain years commercially significant concentrations occur over the western areas of the Scotian Shelf, on Georges Bank and in the Bay of Fundy. As with *Illex*, there is at present no prospect of predicting stock levels in these areas.

Long Term

A greater understanding of the biology of the squids *Illex* and *Loligo* is required to define their population dynamics. As stock size is so variable, more reliable predictors of year-class strength may assist the industry by allowing short-term (months) projections of likely abundance and availability to the fishery.

Squid are part of the food chain at all trophic levels. Their interactions with other commercially important species remains important from both the biological and fisheries viewpoint. Failure to understand their role in the fisheries ecology of the Shelf may seriously hamper effective management of other fisheries resources.

Acknowledgments

The data used to generate the maps and diagrams were obtained from a variety of sources. Bottom trawl groundfish surveys and dedicated squid surveys conducted by Canada, and the U.S.A. (see below). The data set entitled the Scotia-Fundy Region's Squid Program contains data from the Canadian surveys and in addition, results provided from cooperative international squid surveys conducted with the Union of Soviet Socialist Republics, France and Japan. The value of the considerable efforts by the many scientists and personnel who planned and conducted these surveys is greatly appreciated; we thank all those who participated.

Data sources used for analysis within this report.

	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
Research Surveys:																
U.S.A. Groundfish	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Gulf Region Groundfish	●	●	●	●	●	●	●	●	●	●	●	●	○	○	○	○
Scotia-Fundy Region Groundfish	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Scotia-Fundy Region Squid	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	○
Newfoundland Region Squid	○	○	○	○	○	○	○	○	●	●	●	●	●	●	○	○
Canadian Int. Obs. Program	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●

● data available ○ data unavailable

Table 1. Generalized progression of the feeding pattern of *Illex* and *Loligo*. Derived from Amaratunga et al. (1979), Amaratunga (1983), Vovk (1983), Froerman (1984), and Maurer and Bowman (1985).

small juveniles	— chaetognaths and copepods predominate in diet of *Illex* and *Loligo* respectively
	— euphausids, amphipoda, and other small crustacea important
	— as *Illex* grows, chaetognaths become less important and euphausids predominate
large juveniles	— crustacean component is the most important, with euphausids predominating
	— fish, particularly myctophids, and cephalopods become important items in diet
adults	— squid and fish dominate, relative importance varies with availability

Table 2. Northwest Atlantic fish predators of the squids *Illex illecebrosus* and (or) *Loligo pealei*. Source: Mid-Atlantic Fishery Management Council (Anon., 1978) and Lange (1980).

Alewife
American john dory
Atlantic bonito
Atlantic croaker
Atlantic silverside
Atlantic angel shark
Atlantic tomcod
Barndoor skate
Barrelfish
Bigeye thresher shark
Black sea bass
Bluefin tuna
Bluefish
Butterfish
Clearnose skate
Cod
Fourspot flounder
Goosefish
Haddock
Hickory shad
Lancetfish
Little skate
Longhorn sculpin
Mackerel
Mackerel shark
Night shark
Northern pilot whale
Northern searobin
Offshore hake
Opah
Oyster toadfish
Pollock
Rainbow smelt
Red hake
Redfish
Roughtail stingray
Roundnosed grenadier
Sand tiger
Scup
Sea raven
Silver hake
Skipjack tuna
Smooth dogfish
Spiny dogfish
Spotted hake
Striped bass
Summer flounder
Swordfish
Tautog
Thorny skate
Threespine stickleback
Thresher shark
Tilefish
Toadfish
Weakfish
White hake
White marlin
White perch
White shark
Windowpane flounder
Winter skate
Witch flounder
Yellowfin tuna

Table 3. Nominal catches (tonnes) of short-finned squid (*Illex illecebrosus*) in the Northwest Atlantic from 1963 to 1985. Source: Northwest Atl. Fish. Organ. Sci. Counc. Rep., 1980, 1986.

Year	Subarea 2	Subarea 3	Subarea 4	Subarea 5+6
1963	0	2,199	103	1,210
1964	0	10,408	369	193
1965	0	7,831	433	563
1966	0	5,017	201	1,562
1967	0	6,907	126	2,662
1968	0	9	47	4,948
1969	0	21	65	2,802
1970	0	111	1,274	2,453
1971	0	1,607	7,299	4,036
1972	0	26	1,824	14,713
1973	2	620	9,255	15,178
1974	31	17	389	16,653
1975	0	3,764	13,993	13,790
1976	0	11,254	30,510	24,936
1977	6	32,748	47,199	24,883
1978	7	41,369	52,688	17,568
1979	1	88,832	73,259	17,341
1980	1	34,779	34,826	17,864
1981	0	18,061	14,142	15,574
1982	0	11,164	1,744	18,188
1983	0	0	421	11,623
1984	0	368	404	9,876
1985 [9]	—	404	269	6,069

[9] Preliminary data.

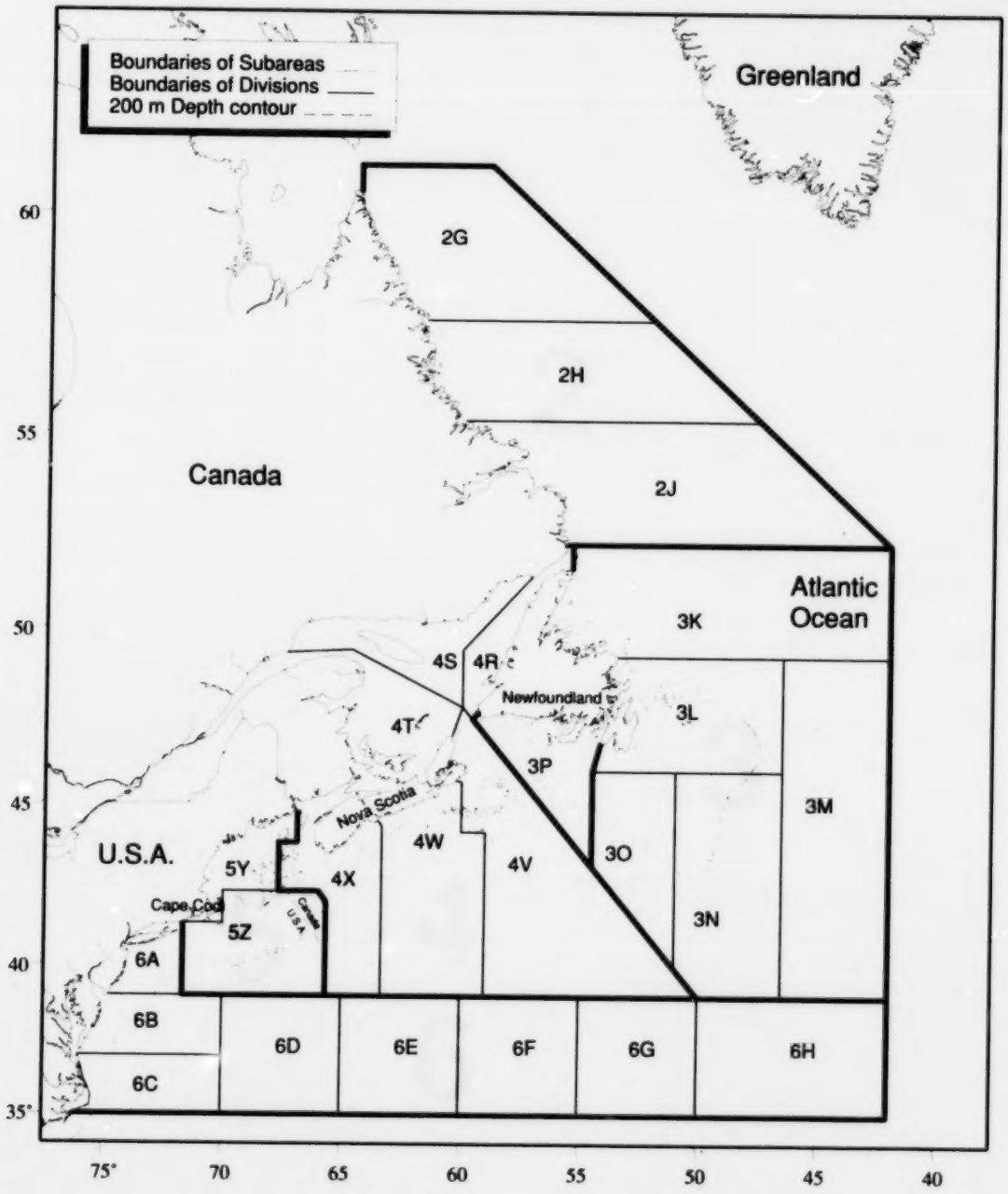


Figure 2. Subareas and Divisions of the NAFO Convention Area.

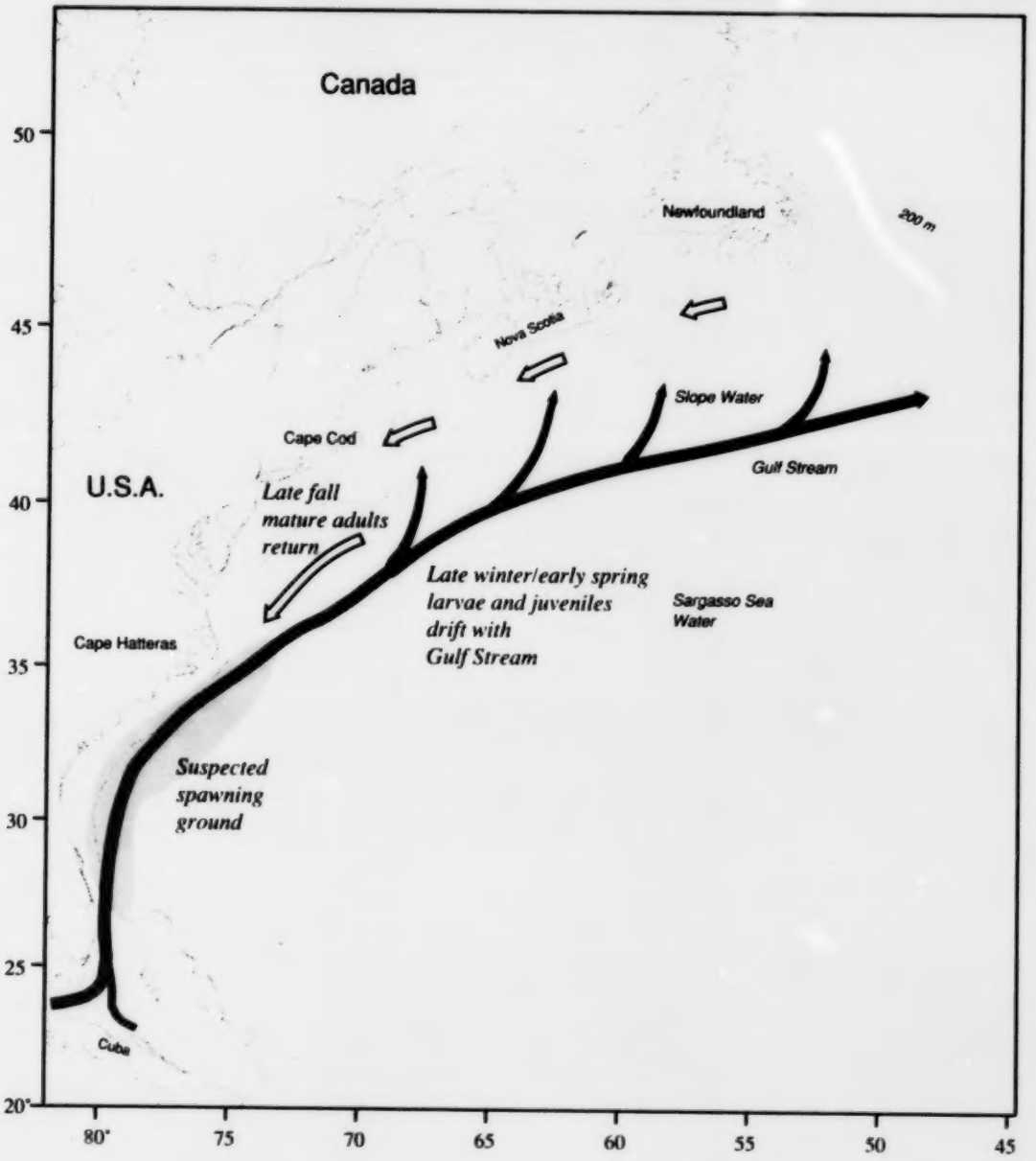


Figure 3. Hypothetical migration path of *Illex illecebrosus* with passive Gulf Stream transport to the northern feeding grounds and active southward migration to the suspected spawning areas south of Cape Hatteras.

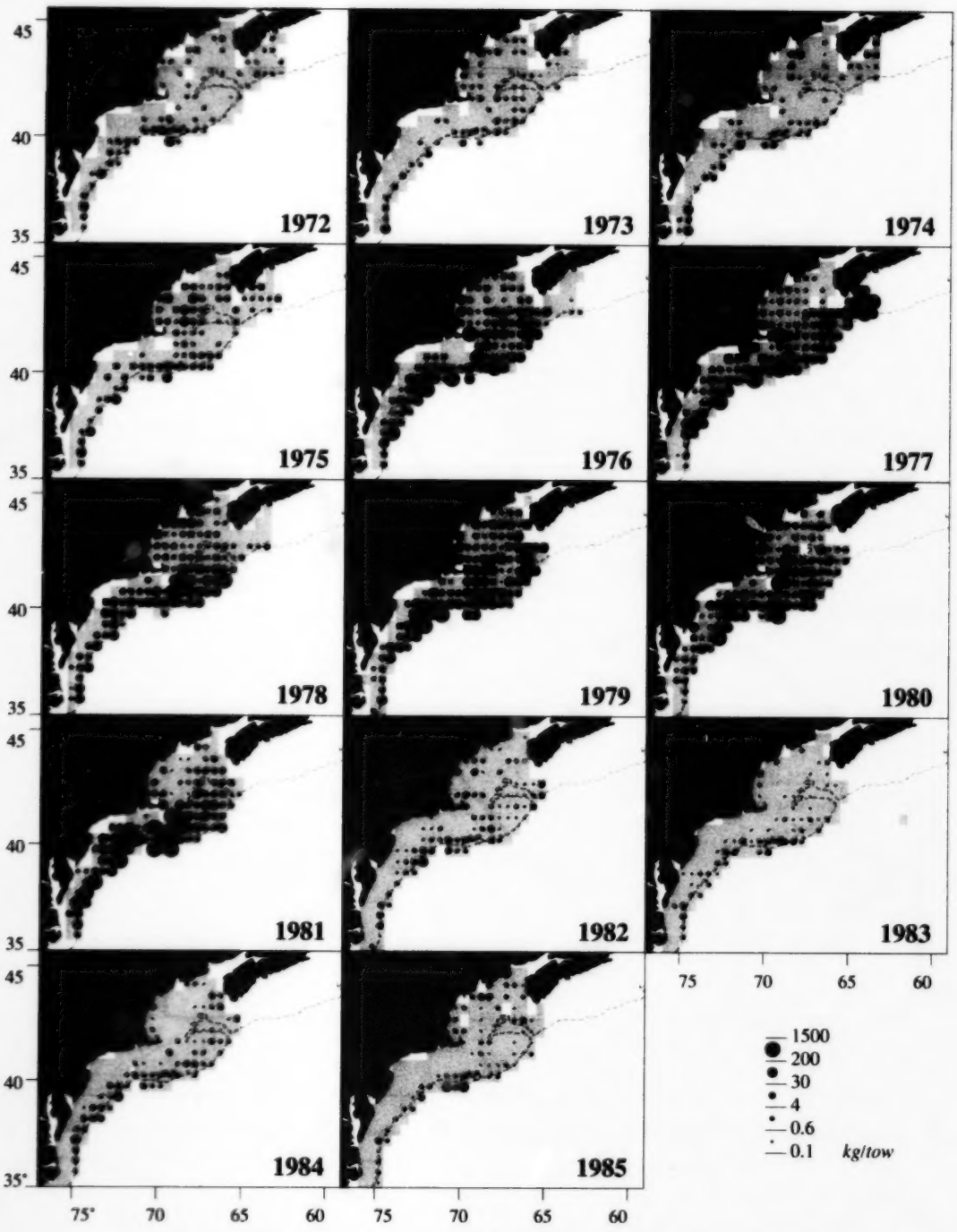


Figure 4. Interannual distribution patterns of *Illex illecebrosus* off the northeastern U.S.A. and western Scotian Shelf between 1972 and 1985, based on data from U.S.A. spring and fall research surveys.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to the catch level.

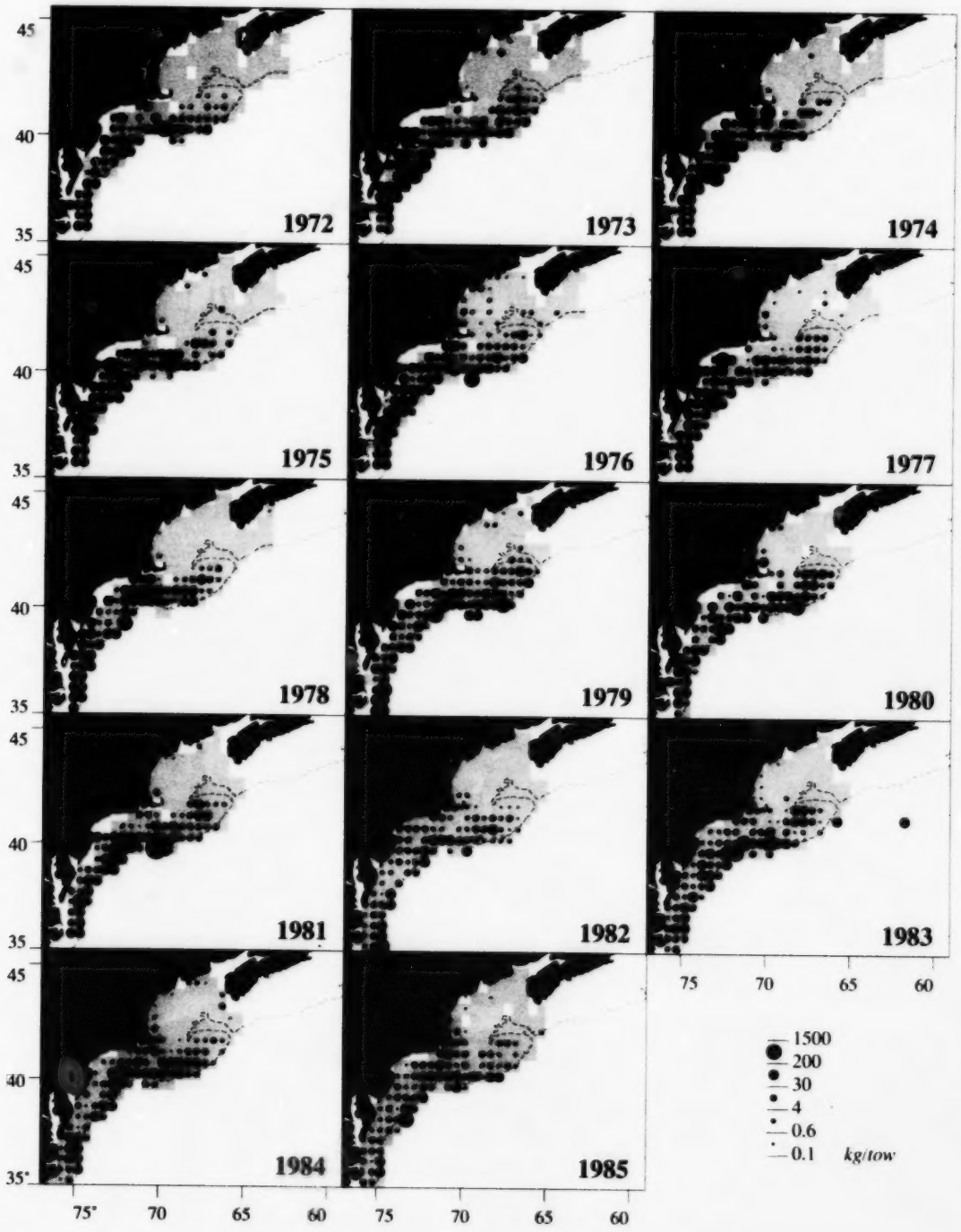


Figure 5. Interannual distribution patterns of *Loligo pealei* off the northeastern U.S.A. and western Scotian Shelf between 1972 and 1985, based on data from U.S.A. spring and fall research surveys.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to the catch level.

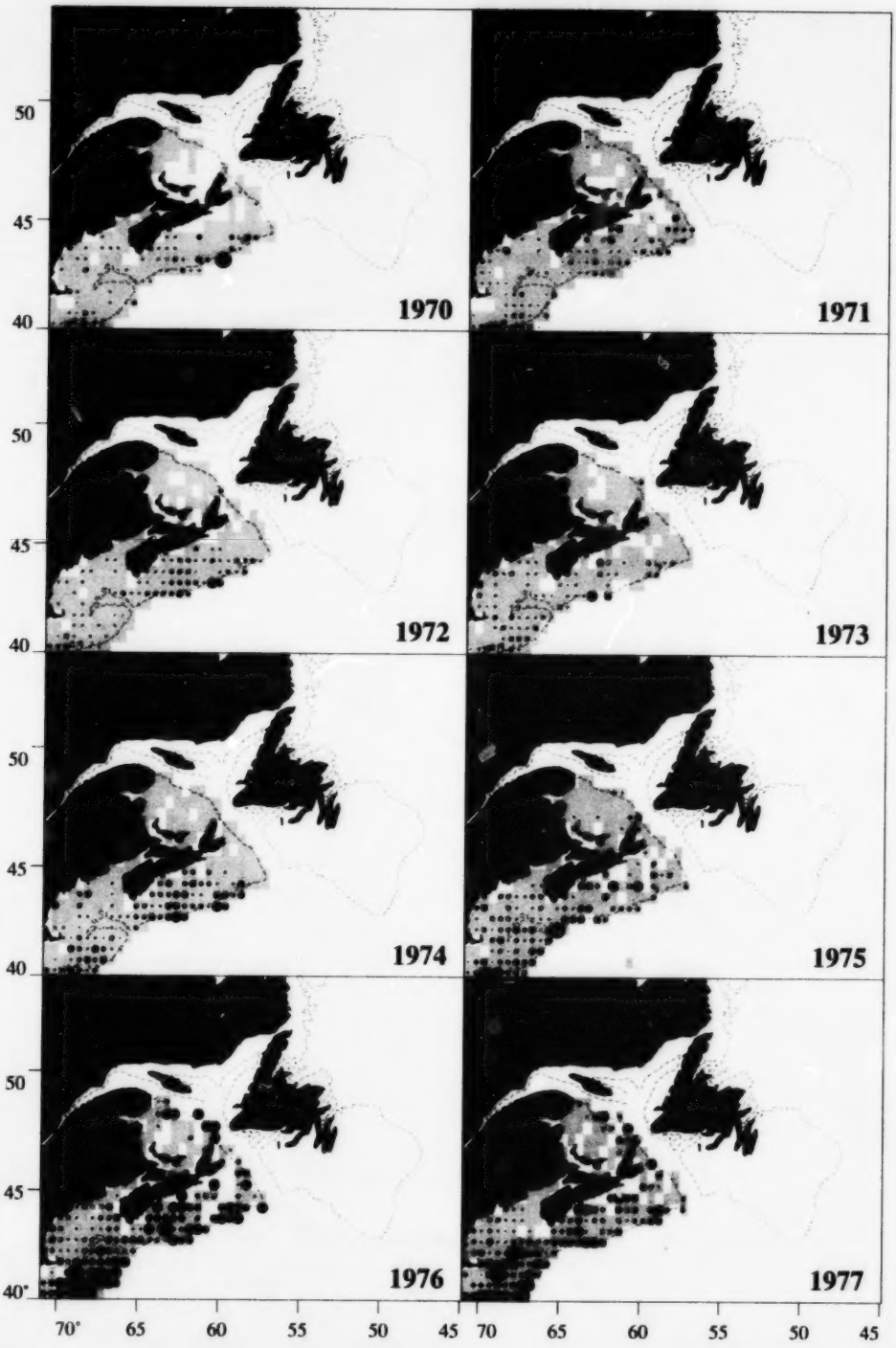


Figure 6. Interannual distributional patterns of *Illex illecebrosus* off eastern Canada and the northeastern U.S.A. between 1970 and 1985, based on data from Canadian spring, summer, and fall research surveys, and spring and fall U.S.A. research surveys.

Area sampled is indicated by by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to the catch level.

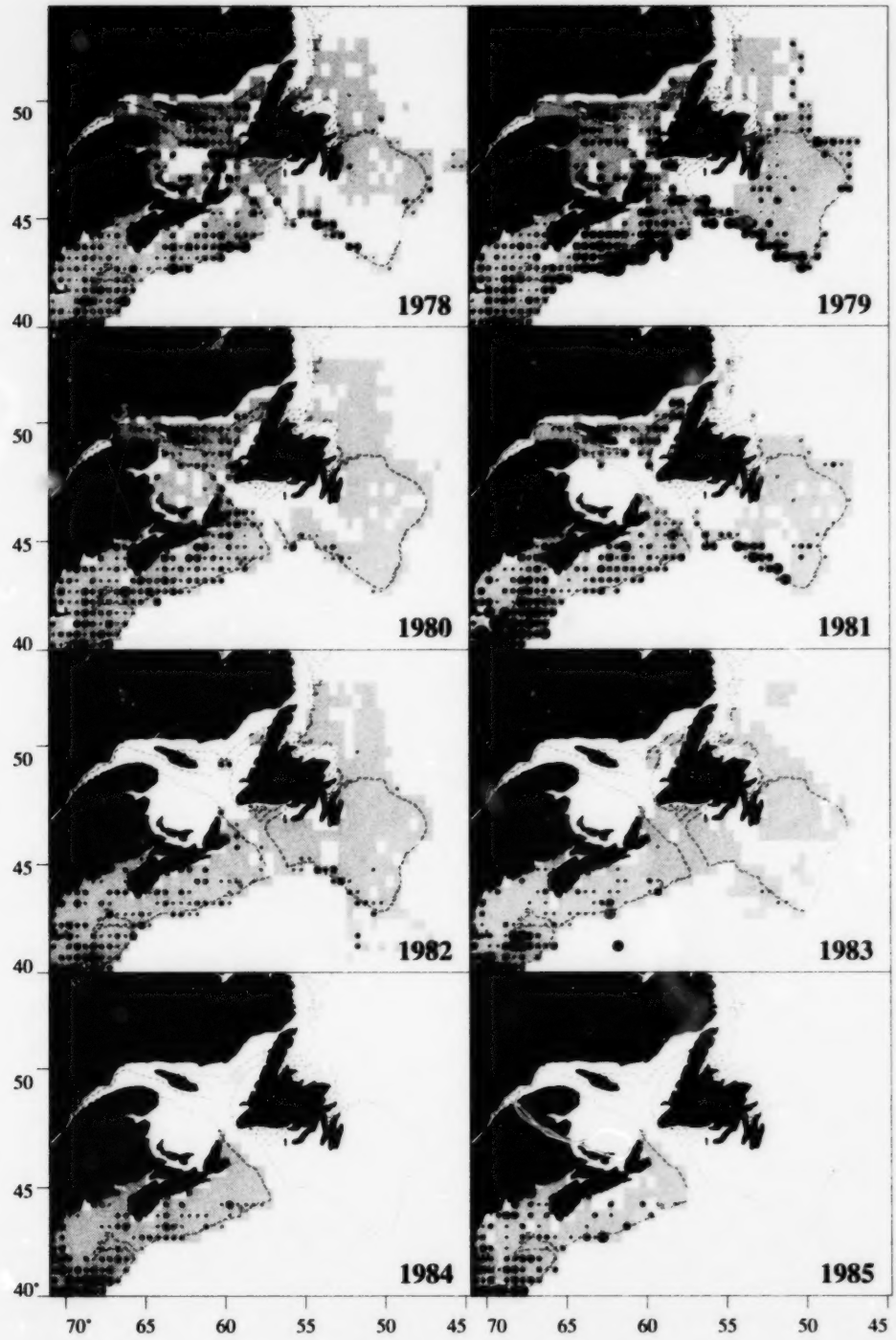


Figure 6 cont. Interannual distribution patterns of *Illex illecebrosus* off eastern Canada and the north-eastern U.S.A. between 1970 and 1985, based on data from Canadian spring, summer, and fall research surveys, and spring and fall U.S.A. research surveys.

Note: A corresponding figure for *Loligo pealei* is not presented, as it seldom occurs on the Scotian Shelf in significant numbers.

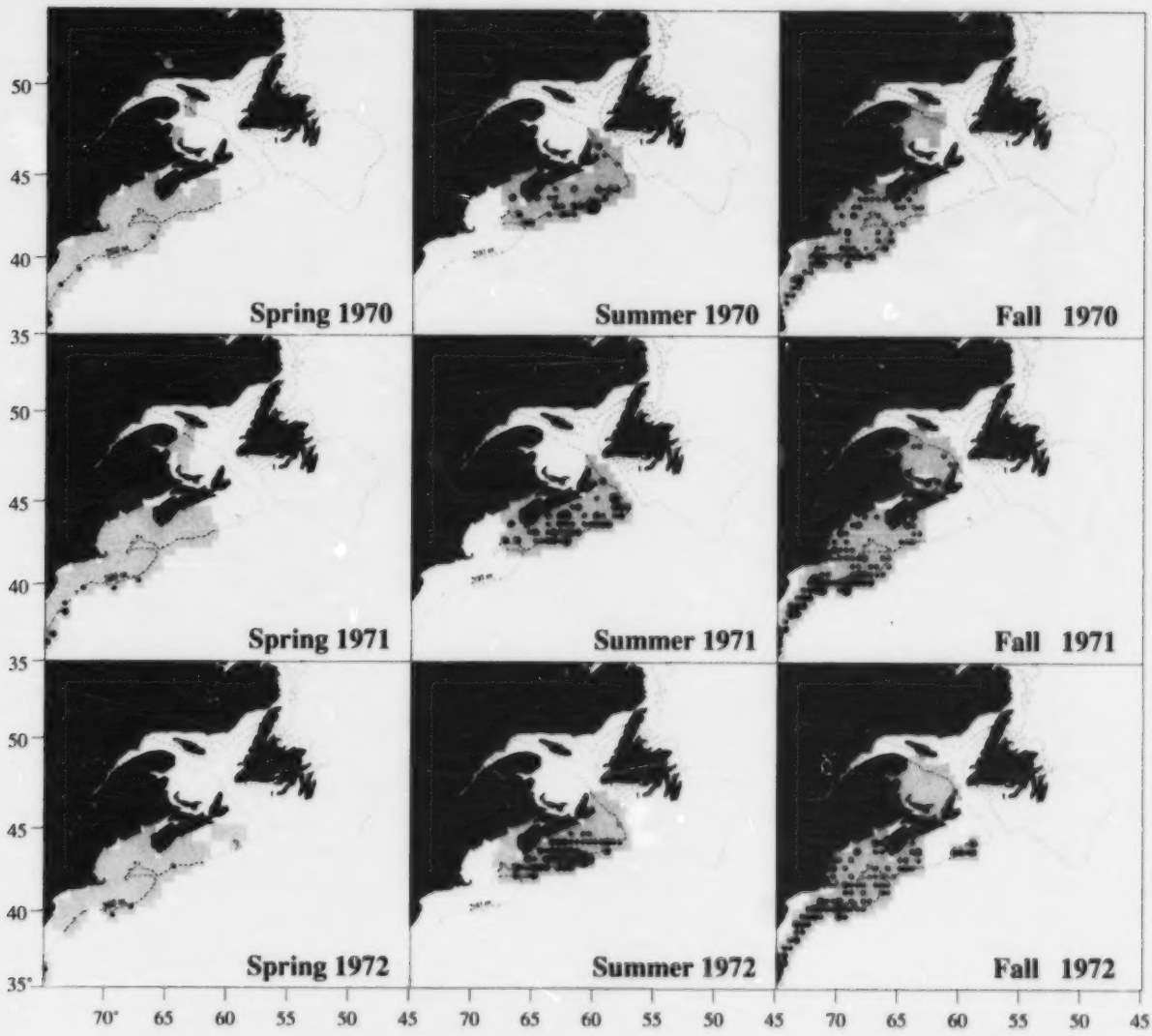


Figure 7. Seasonal distribution patterns of *Illex illecebrosus* off the eastern U.S.A. and Canada between 1970 and 1980. Based on data from U.S.A. and Canadian research surveys.

Area sampled is indicated by shading, and mean catch in kg/tow for each 1° square is represented by a solid circle scaled to catch level.

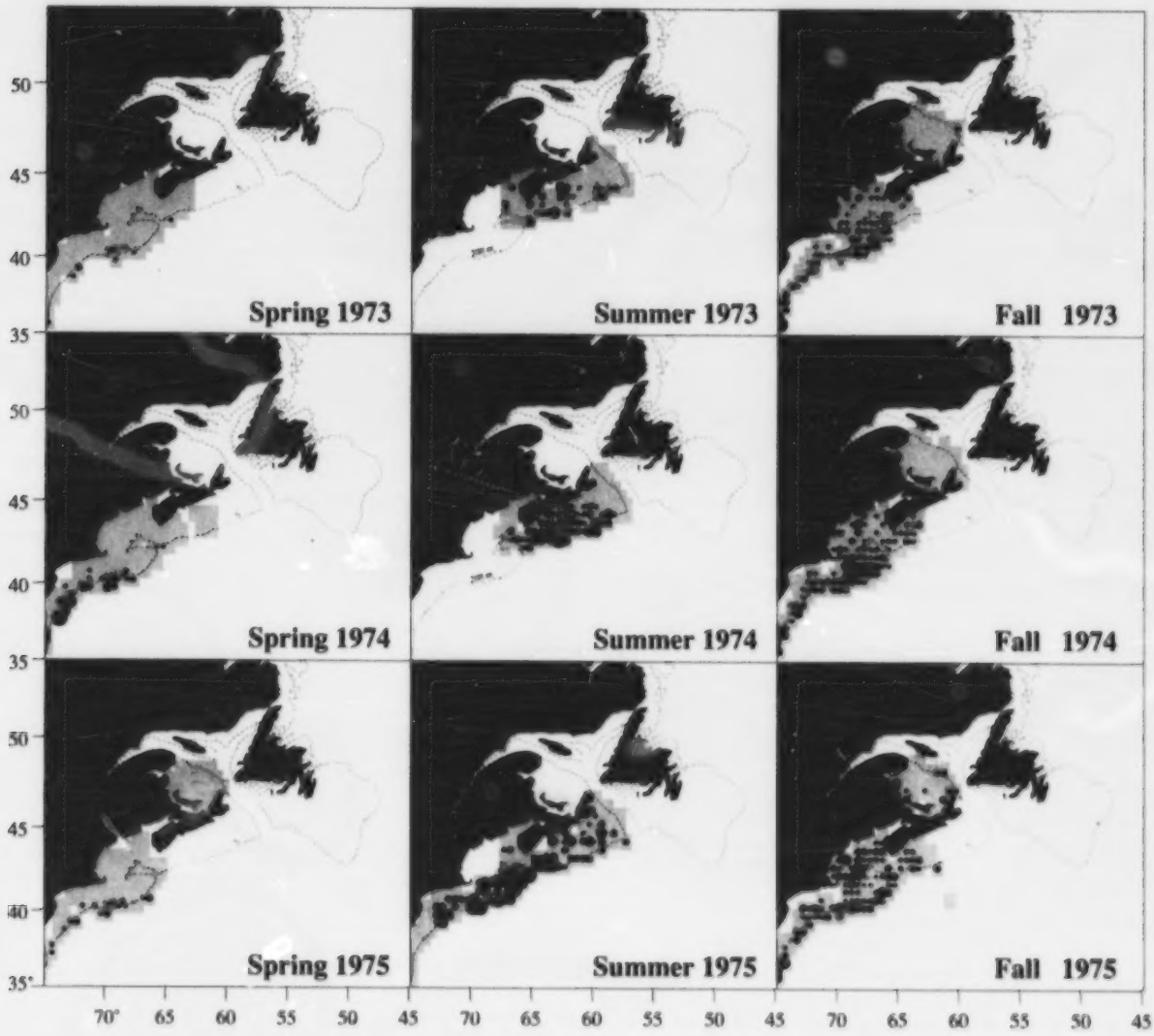


Figure 7 cont. Seasonal distribution patterns of *Illex illecebrosus* off the eastern U.S.A. and Canada between 1970 and 1980. Based on data from U.S.A. and Canadian research surveys.

Area sampled is indicated by shading, and mean catch in kg/tow for each 1° square is represented by a solid circle scaled to catch level.

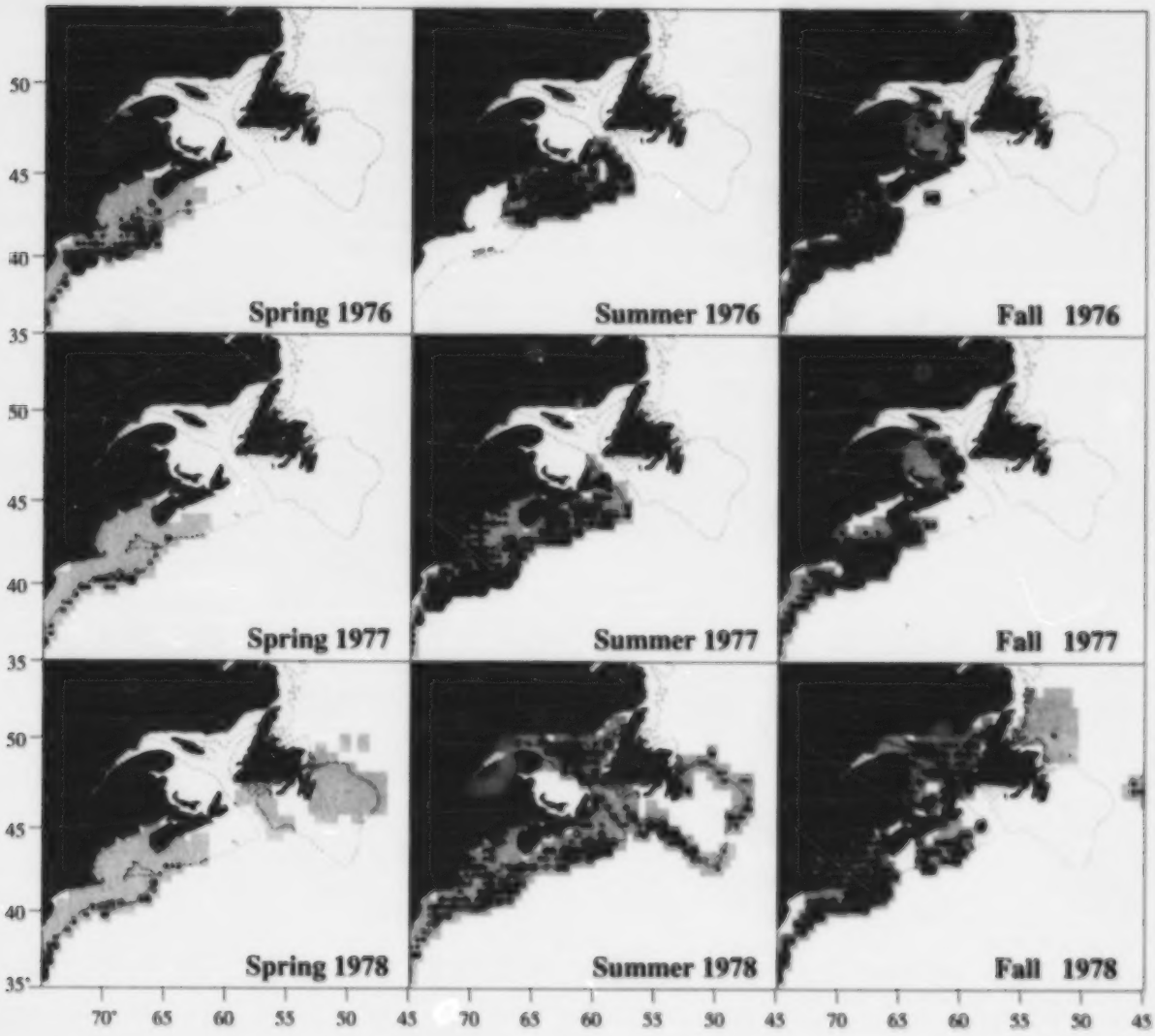


Figure 7 cont. Seasonal distribution patterns of *Illex illecebrosus* off the eastern U.S.A. and Canada between 1970 and 1980. Based on data from U.S.A. and Canadian research surveys.

Area sampled is indicated by shading, and mean catch in kg/tow for each 1° square is represented by a solid circle scaled to catch level.

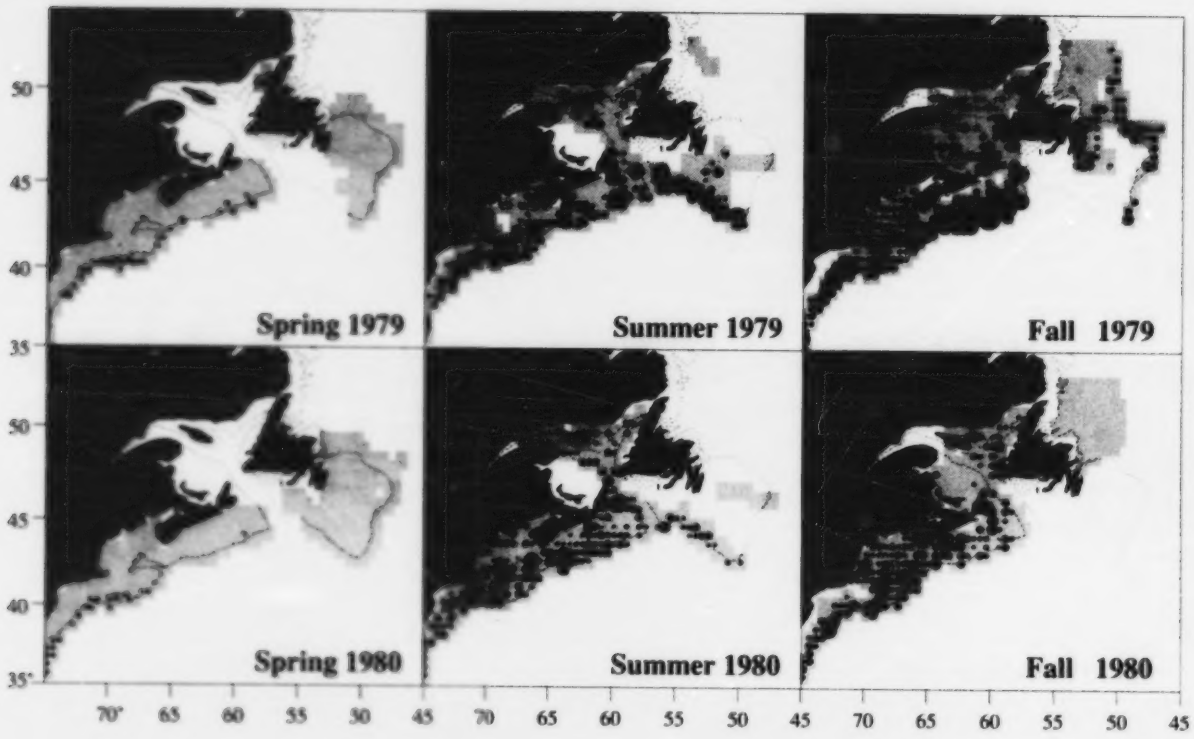


Figure 7 cont. Seasonal distribution patterns of *Illex illecebrosus* off the eastern U.S.A. and Canada between 1970 and 1980. Based on data from U.S.A. and Canadian research surveys.

Area sampled is indicated by shading, and mean catch in kg/tow for each 1° square is represented by a solid circle scaled to catch level.

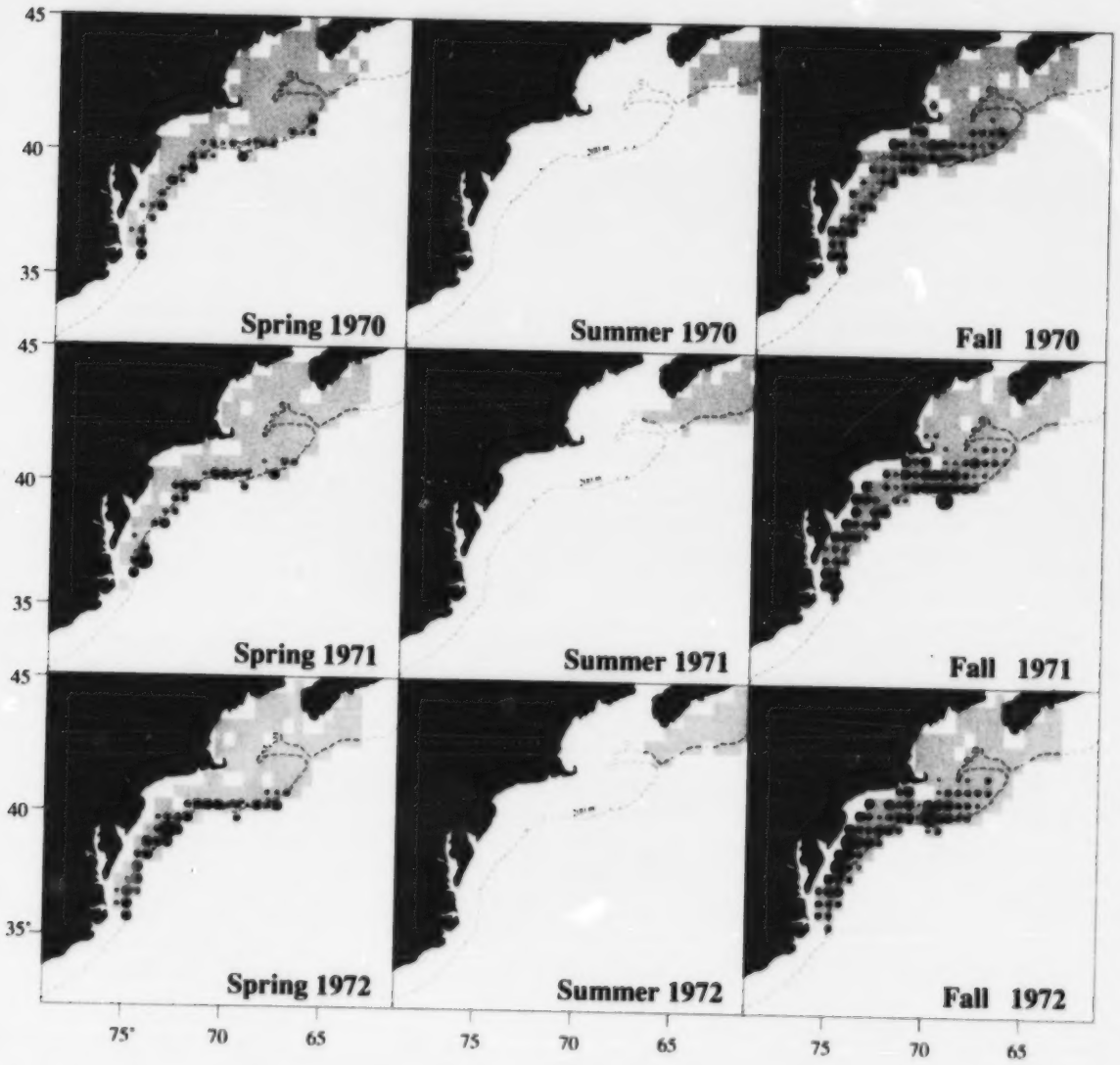


Figure 8. Seasonal distribution patterns of *Loligo pealei* off the eastern U.S.A. and Canada between 1970 and 1980. Based on data from U.S.A. and Canadian research surveys.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to catch level.

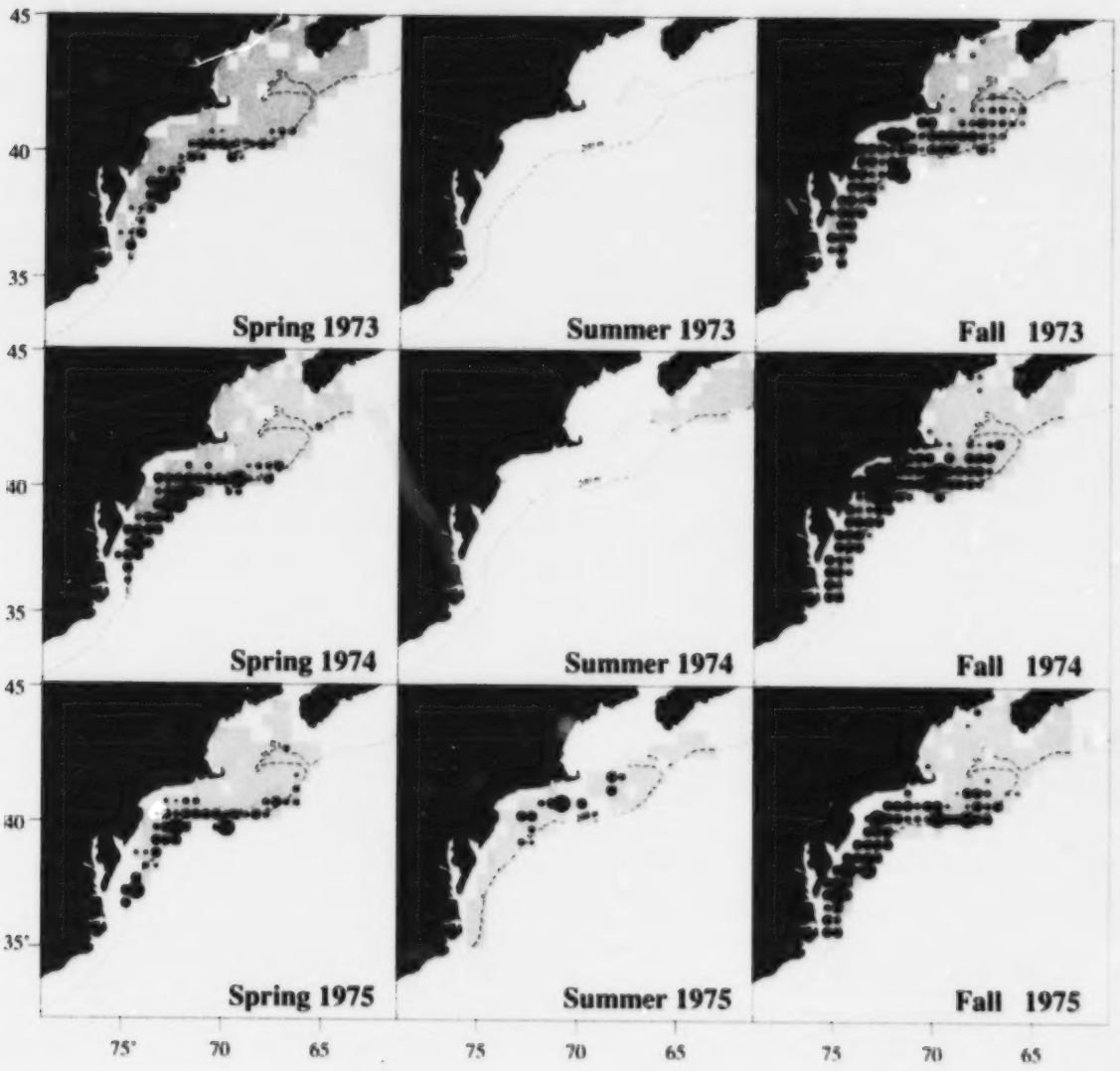


Figure 8 cont. Seasonal distribution patterns of *Loligo pealei* off the eastern U.S.A. and Canada between 1970 and 1980. Based on data from U.S.A. and Canadian research surveys.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to catch level.

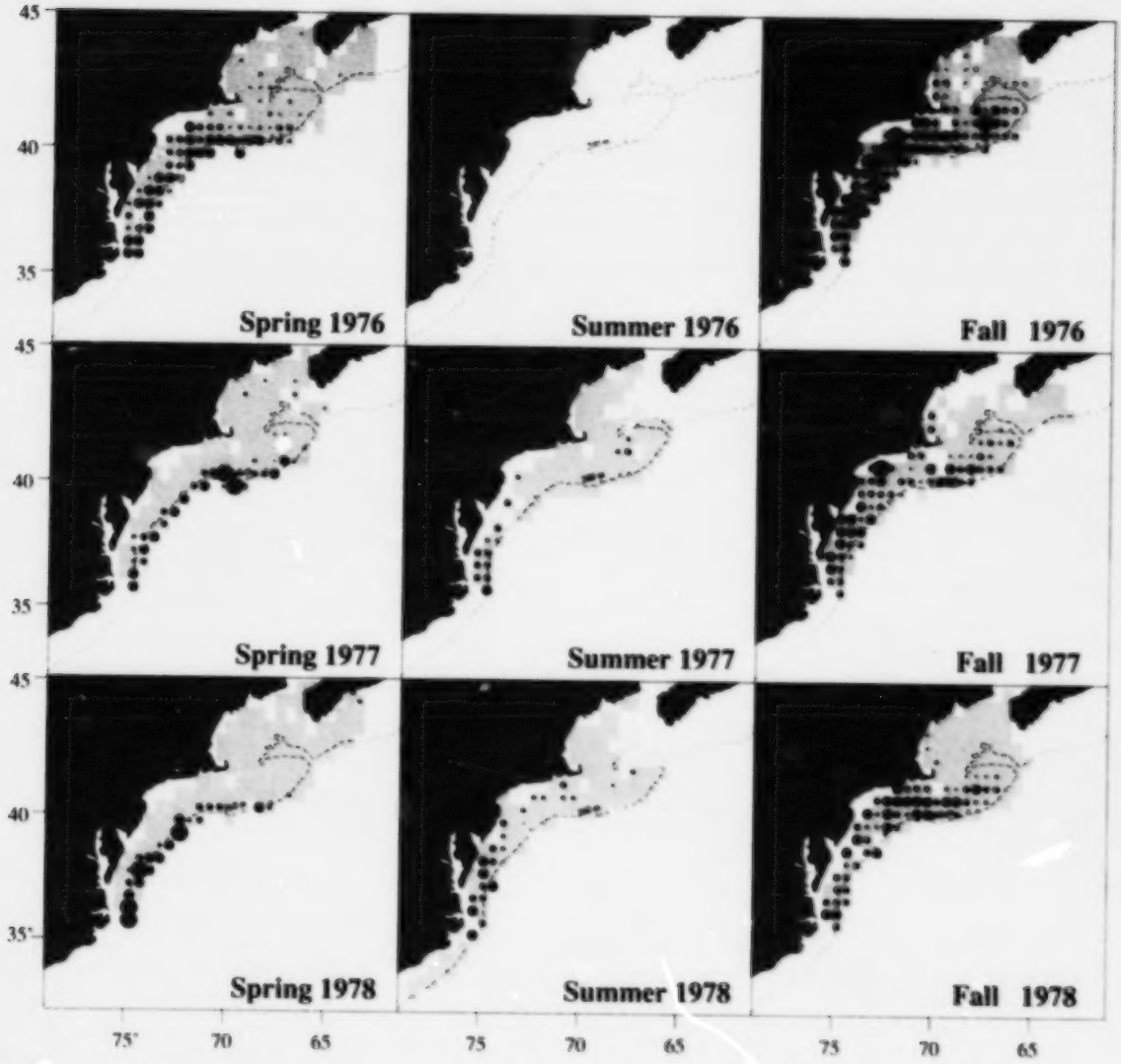


Figure 8 cont. Seasonal distribution patterns of *Loligo pealei* off the eastern U.S.A. and Canada between 1970 and 1980. Based on data from U.S.A. and Canadian research surveys.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to catch level.

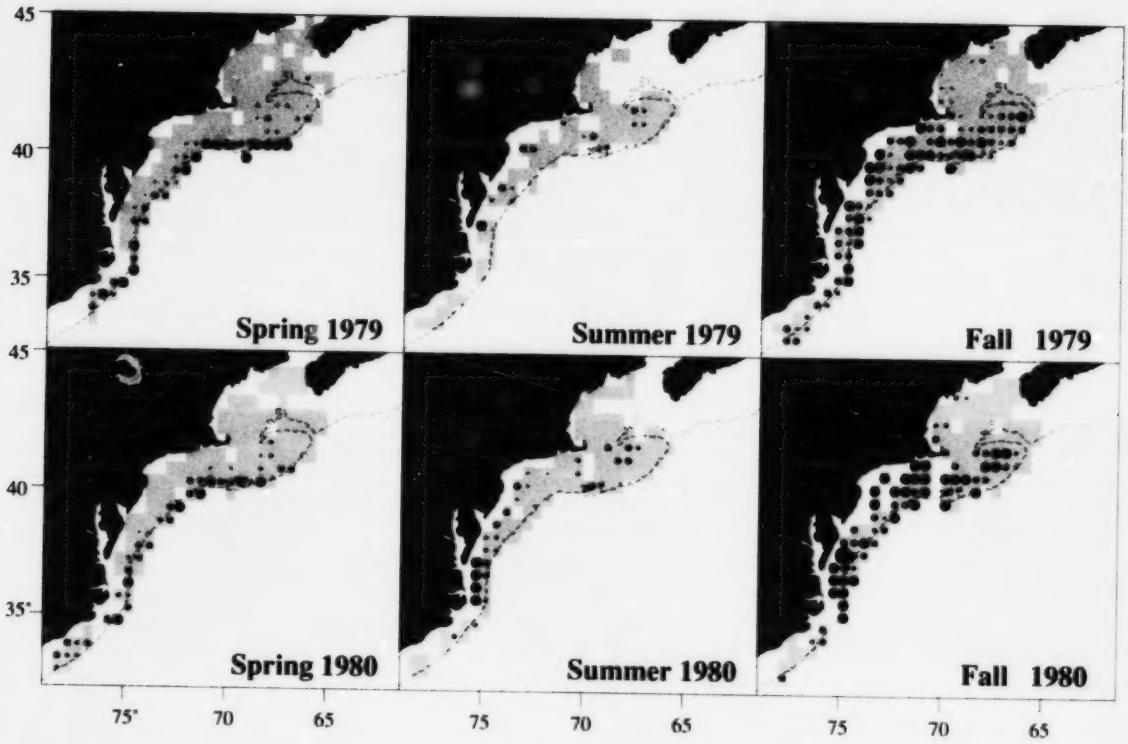


Figure 8 cont. Seasonal distribution patterns of *Loligo pealei* off the eastern U.S.A. and Canada between 1970 and 1980. Based on data from U.S.A. and Canadian research surveys.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to catch level.

250
30
5
0.7
0.1 *kg/tow*

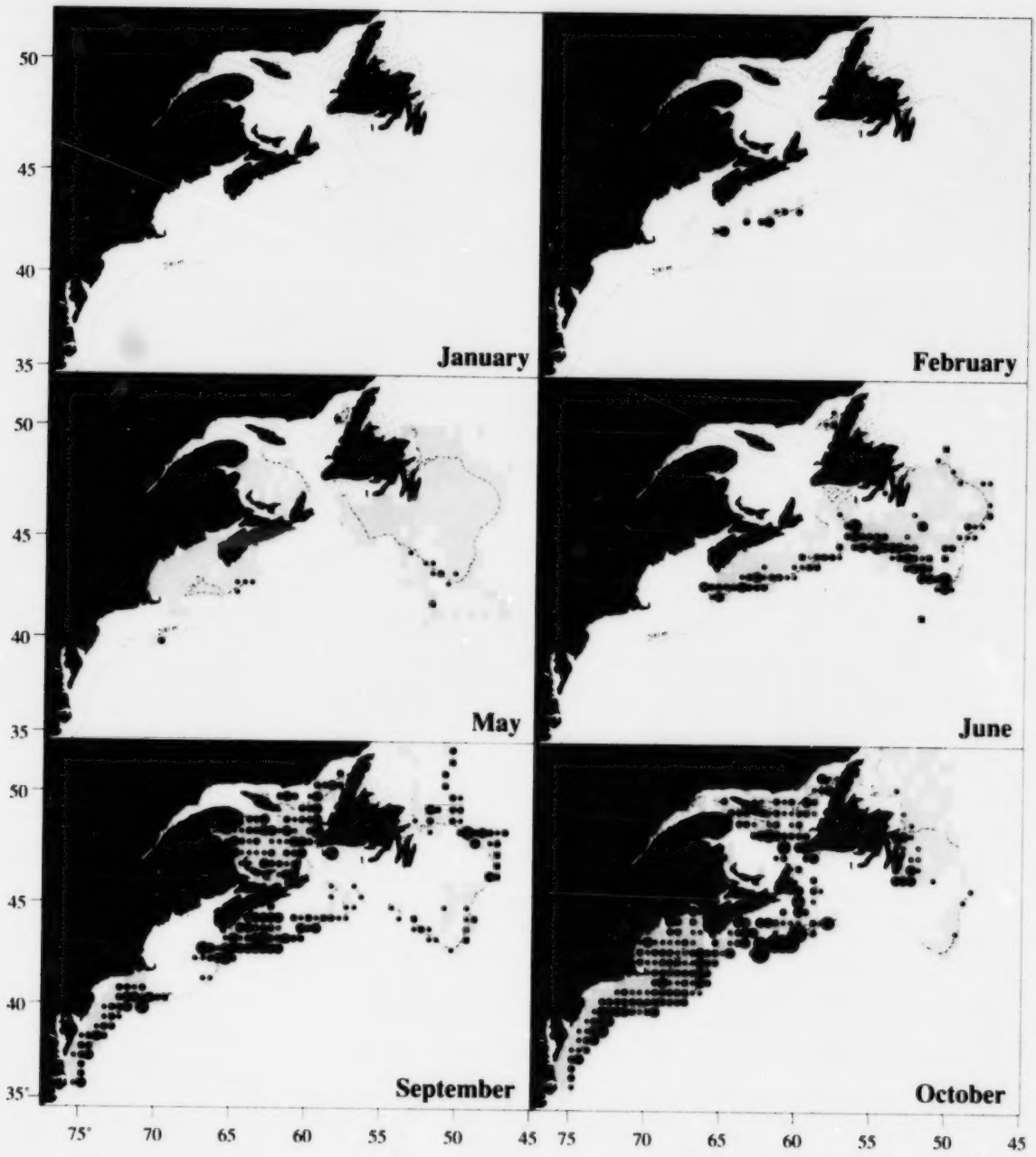


Figure 9. Monthly distribution patterns of *Illex illecebrosus* off the eastern U.S.A. and Canada for the period 1970-80. Based on data from U.S.A. and Canadian research surveys.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to catch level.

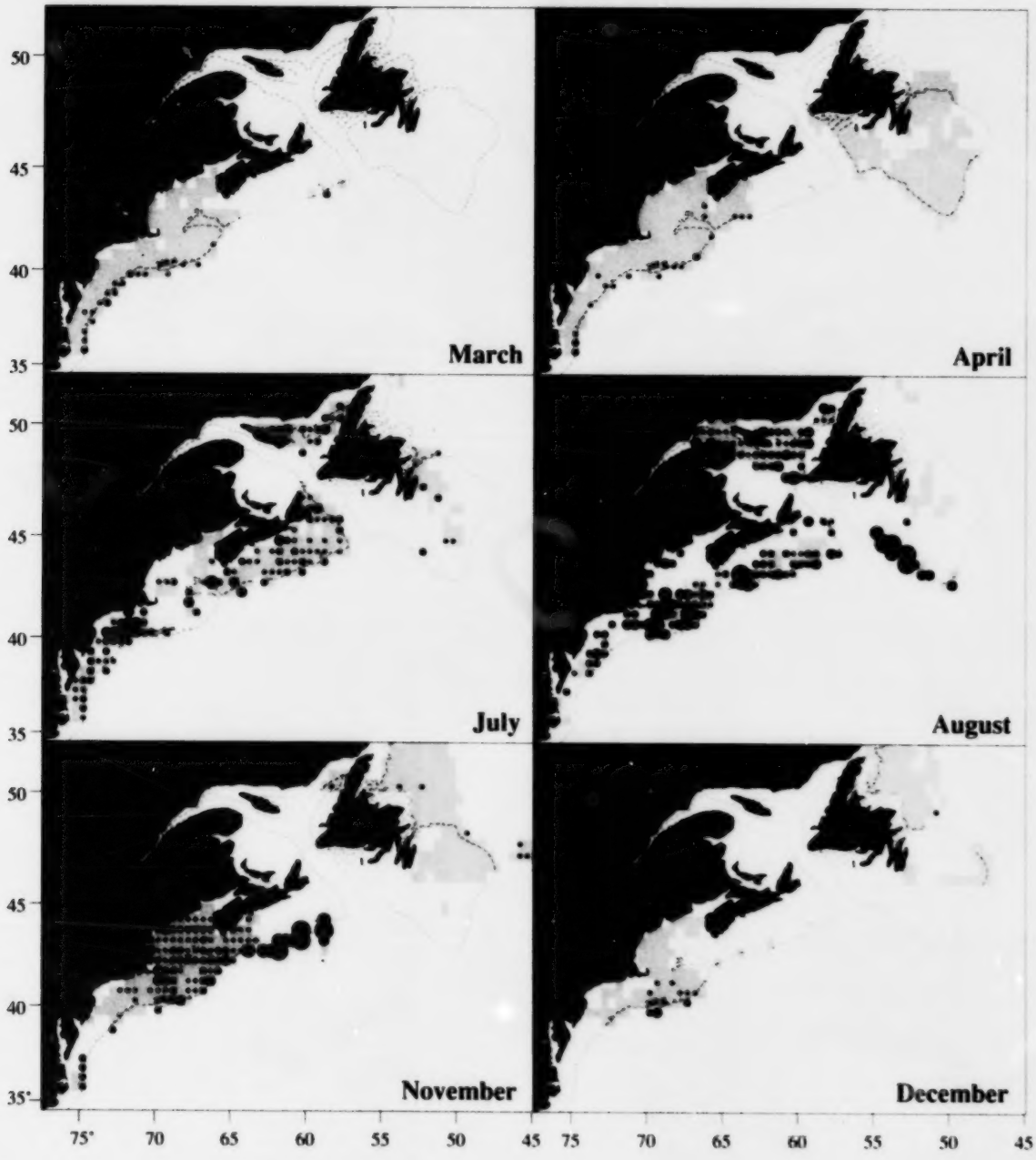


Figure 9 cont. Monthly distribution patterns of *Illex illecebrosus* off the eastern U.S.A. and Canada for the period 1970-80. Based on data from U.S.A. and Canadian research surveys.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to catch level.

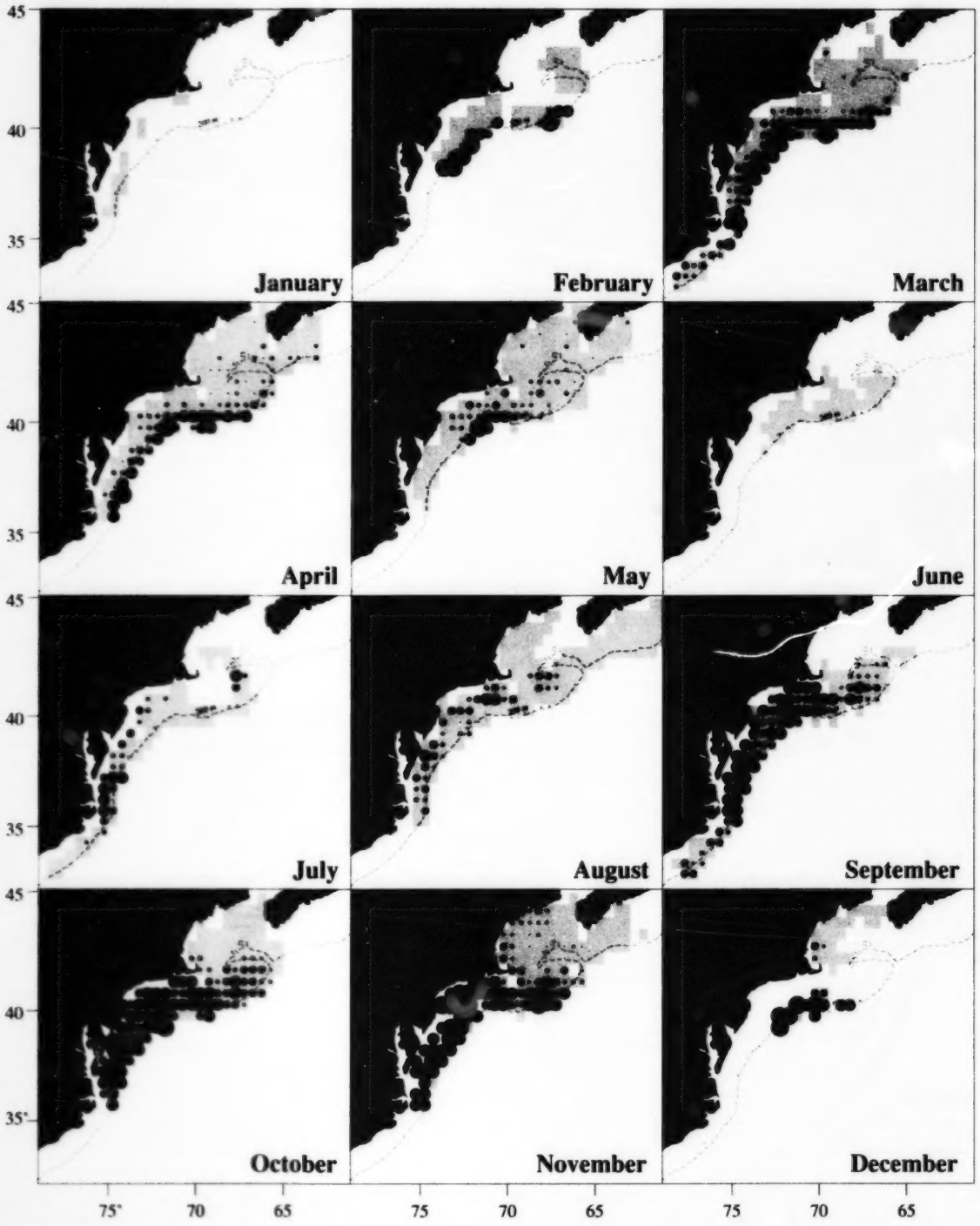


Figure 10. Monthly distribution patterns of *Loligo pealei* off the eastern U.S.A. for the period 1970-80. Based on data from U.S.A. and Canadian research surveys.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to catch level.

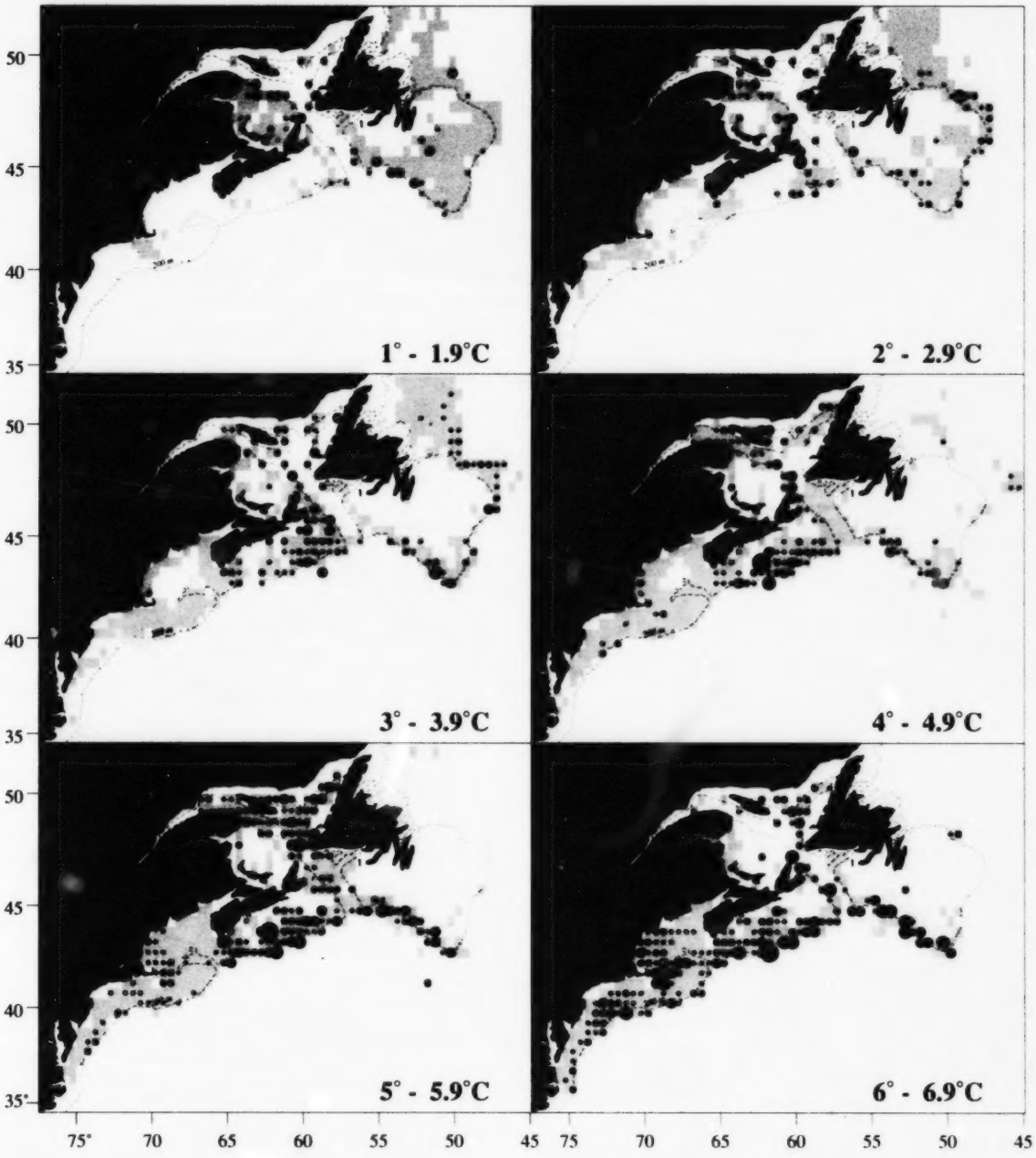


Figure 11. Distribution of *Illex illecebrosus* in relation to bottom temperature. Based on data from U.S.A. and Canadian research surveys for the period 1970-80.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to catch level.

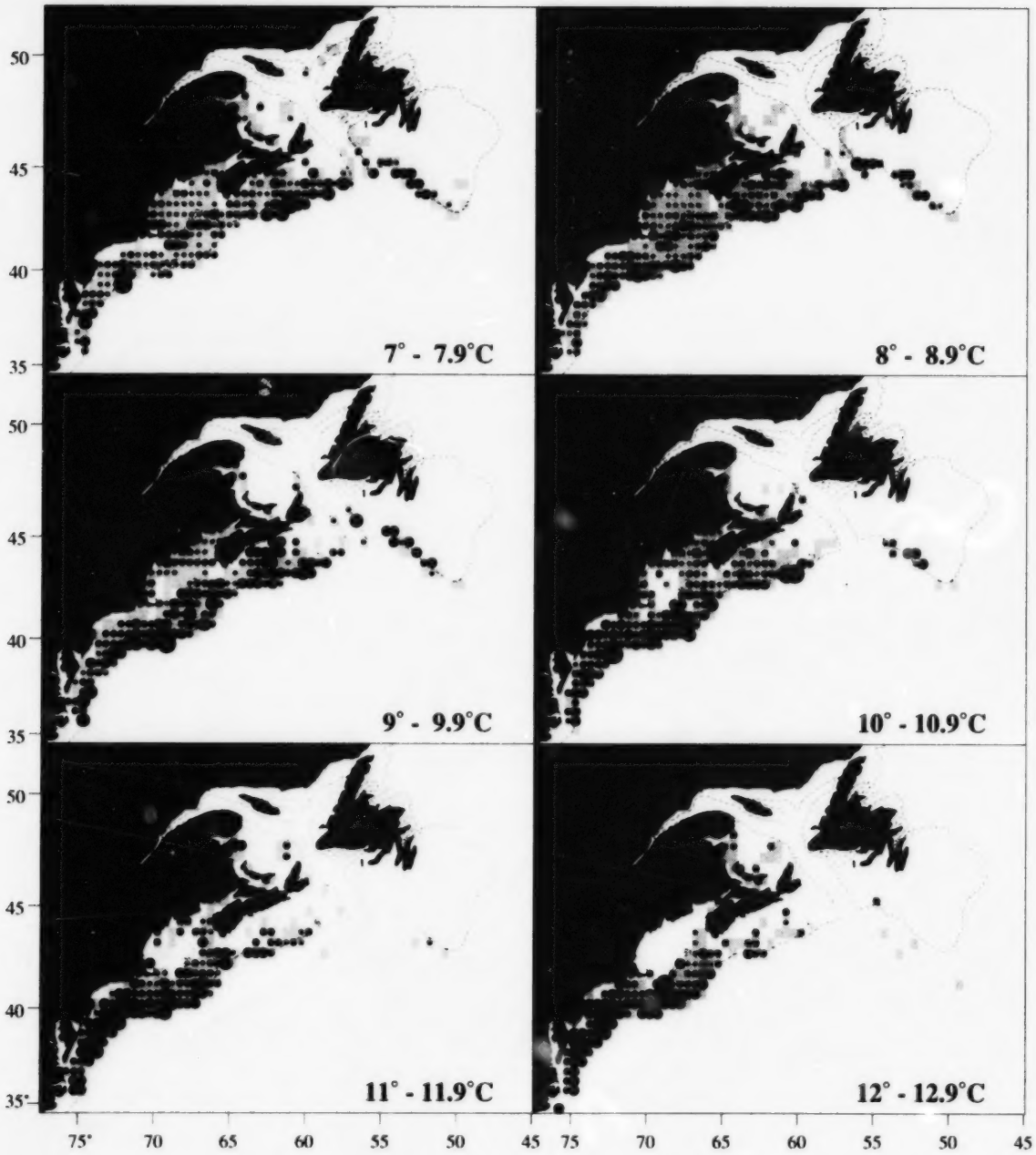


Figure 11 cont. Distribution of *Illex illecebrosus* in relation to bottom temperature. Based on data from U.S.A. and Canadian research surveys for the period 1970-80.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to catch level.

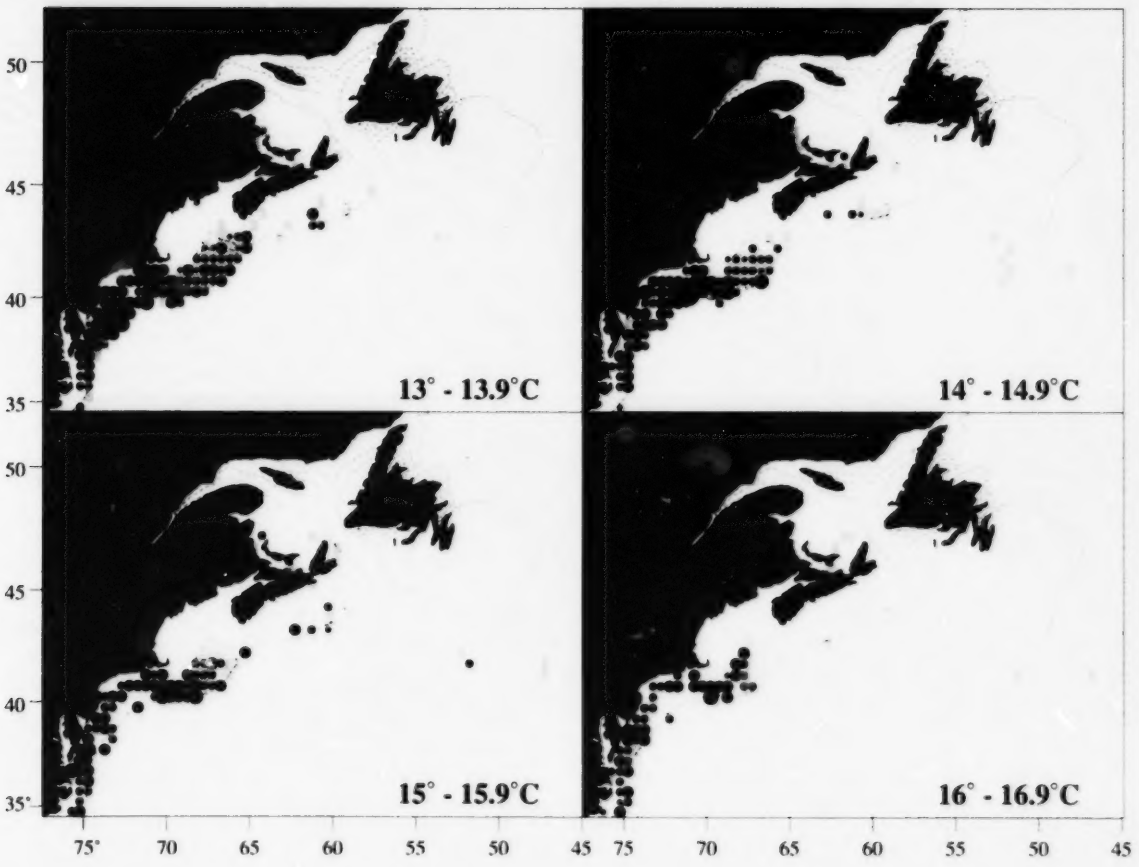


Figure 11 cont. Distribution of *Illex illecebrosus* in relation to bottom temperature. Based on data from U.S.A. and Canadian research surveys for the period 1970-80.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to catch level.

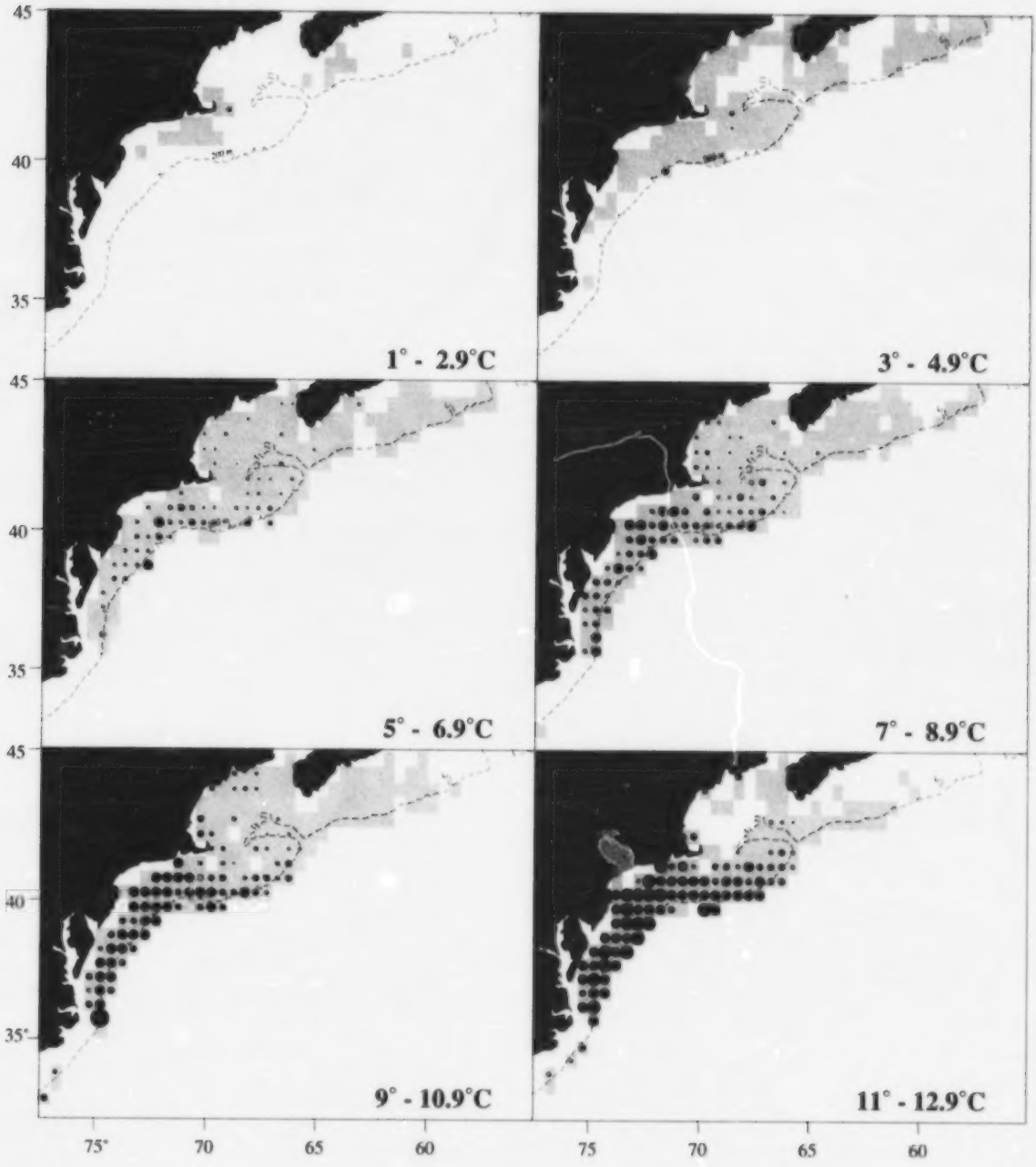


Figure 12. Distribution of *Loligo pealei* in relation to bottom temperature. Based on data from U.S.A. research surveys for the period 1970-80.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to catch level.

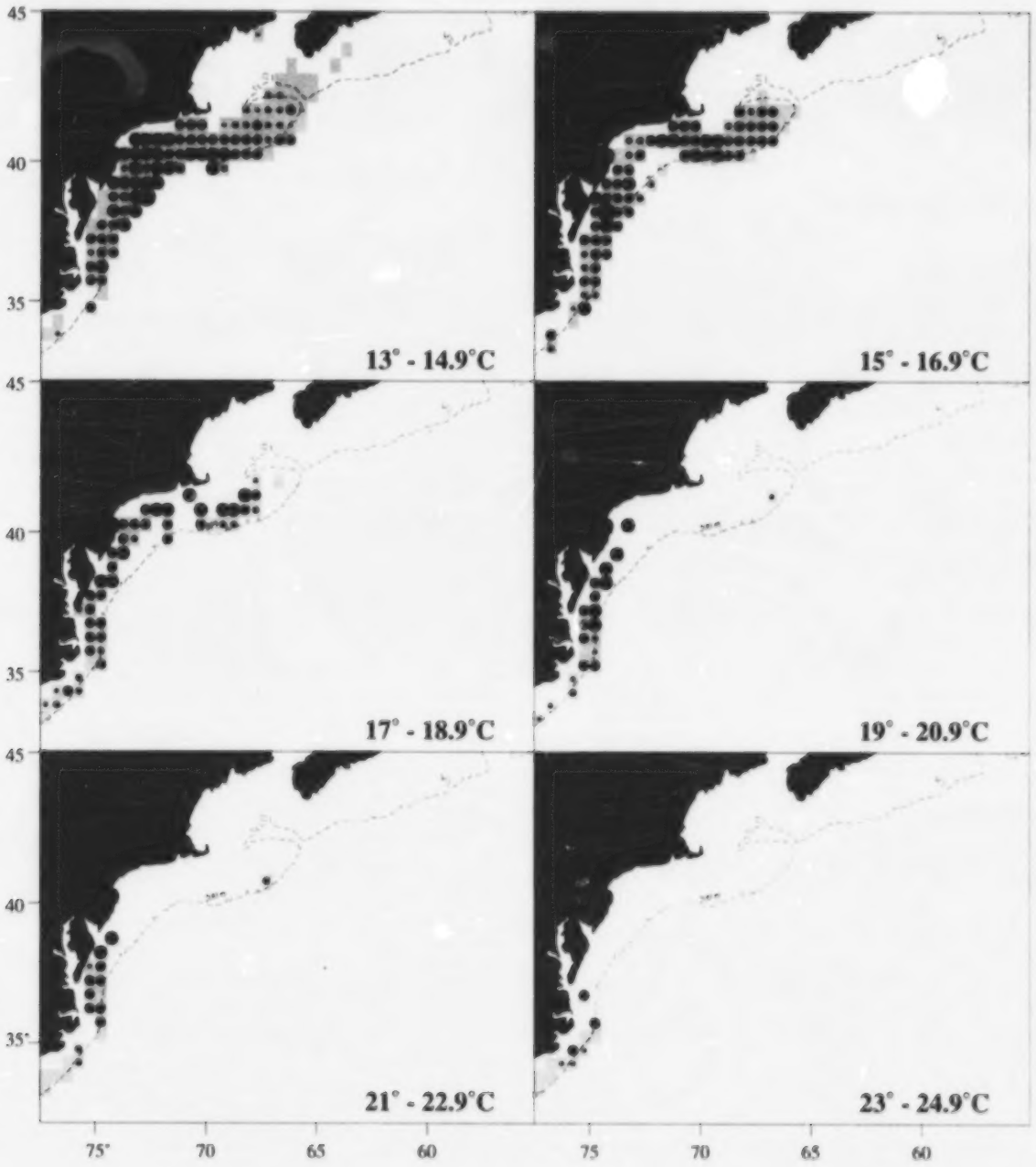


Figure 12 cont. Distribution of *Loligo pealei* in relation to bottom temperature. Based on data from U.S.A. research surveys for the period 1970-80.

Area sampled is indicated by shading, and mean catch in kg/tow for each 0.5° square is represented by a solid circle scaled to catch level.

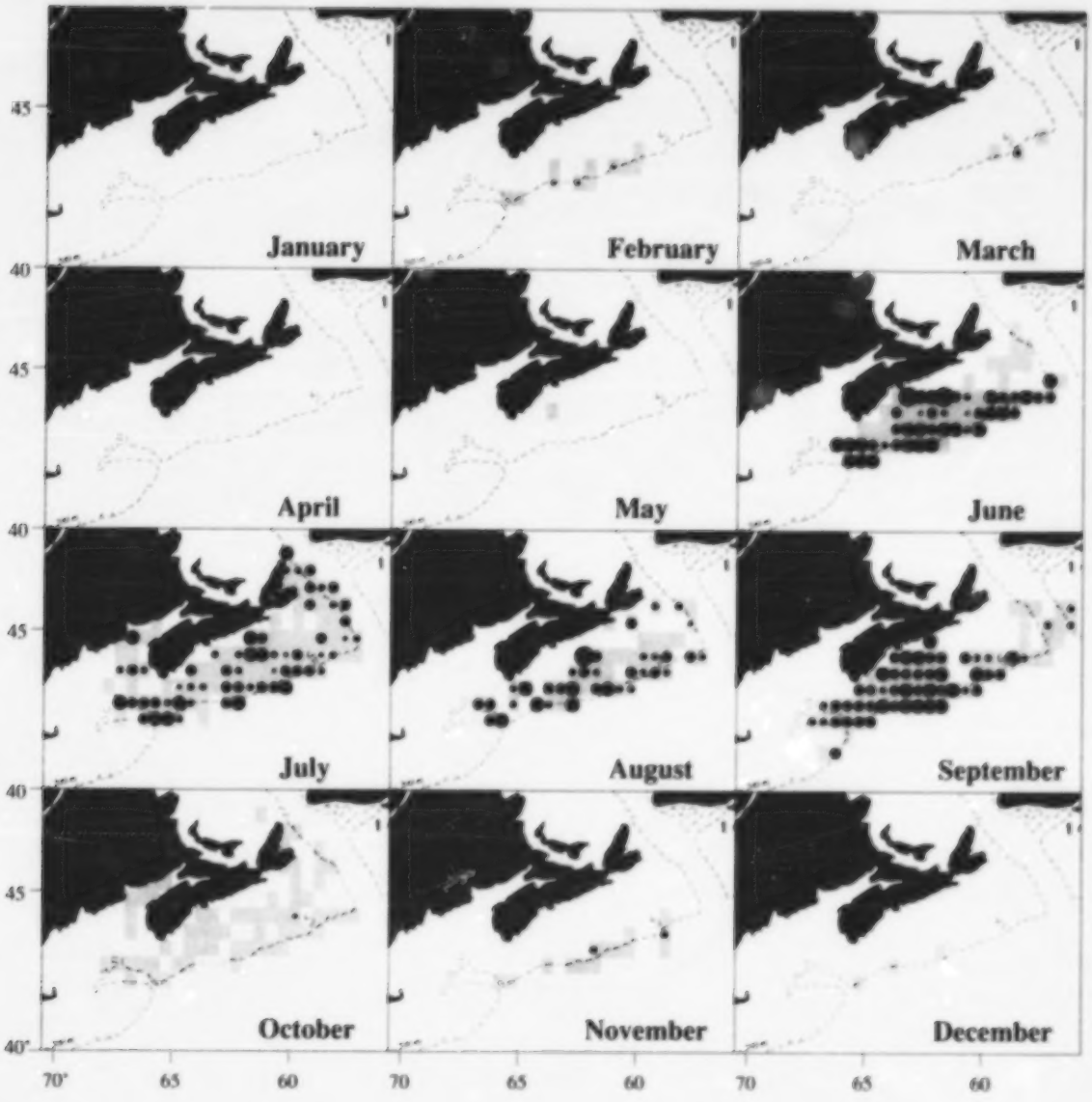


Figure 13. Monthly pattern of distribution over the Scotian Shelf of immature male *Illex illecebrosus* during the period 1970-83.

Area sampled is indicated by shading, and mean catch in number of animals per tow for each 0.5° square is represented by a solid circle scaled to catch level.

Note: A similar figure is not presented for *Loligo pealei* in view of the generally limited distribution of this species over the Scotian shelf.

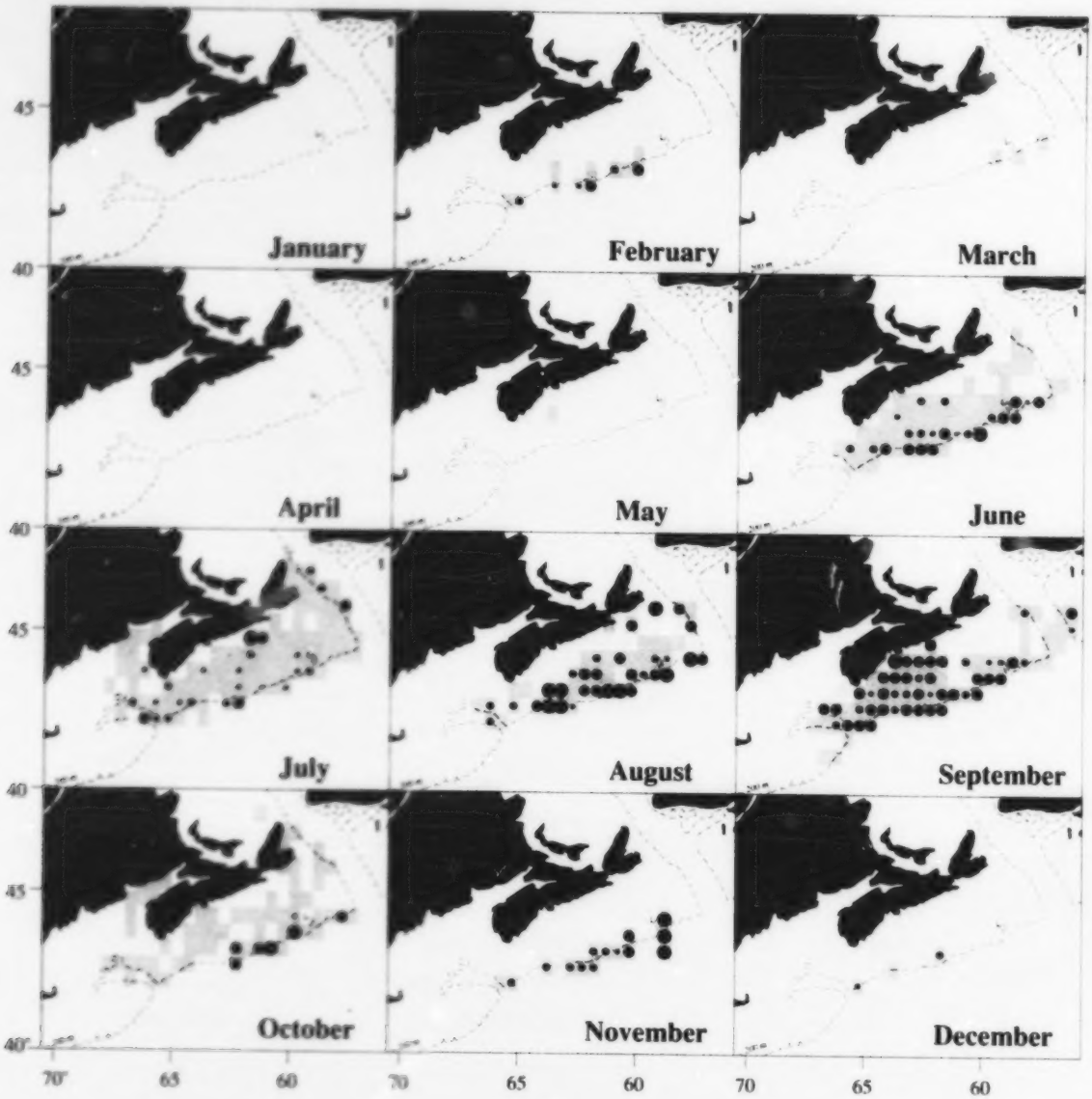


Figure 13 cont. Monthly pattern of distribution over the Scotian Shelf of maturing male *Illex illecebrosus* during the period 1970-83.

Area sampled is indicated by shading, and mean catch in number of animals per tow for each 0.5° square is represented by a solid circle scaled to catch level.

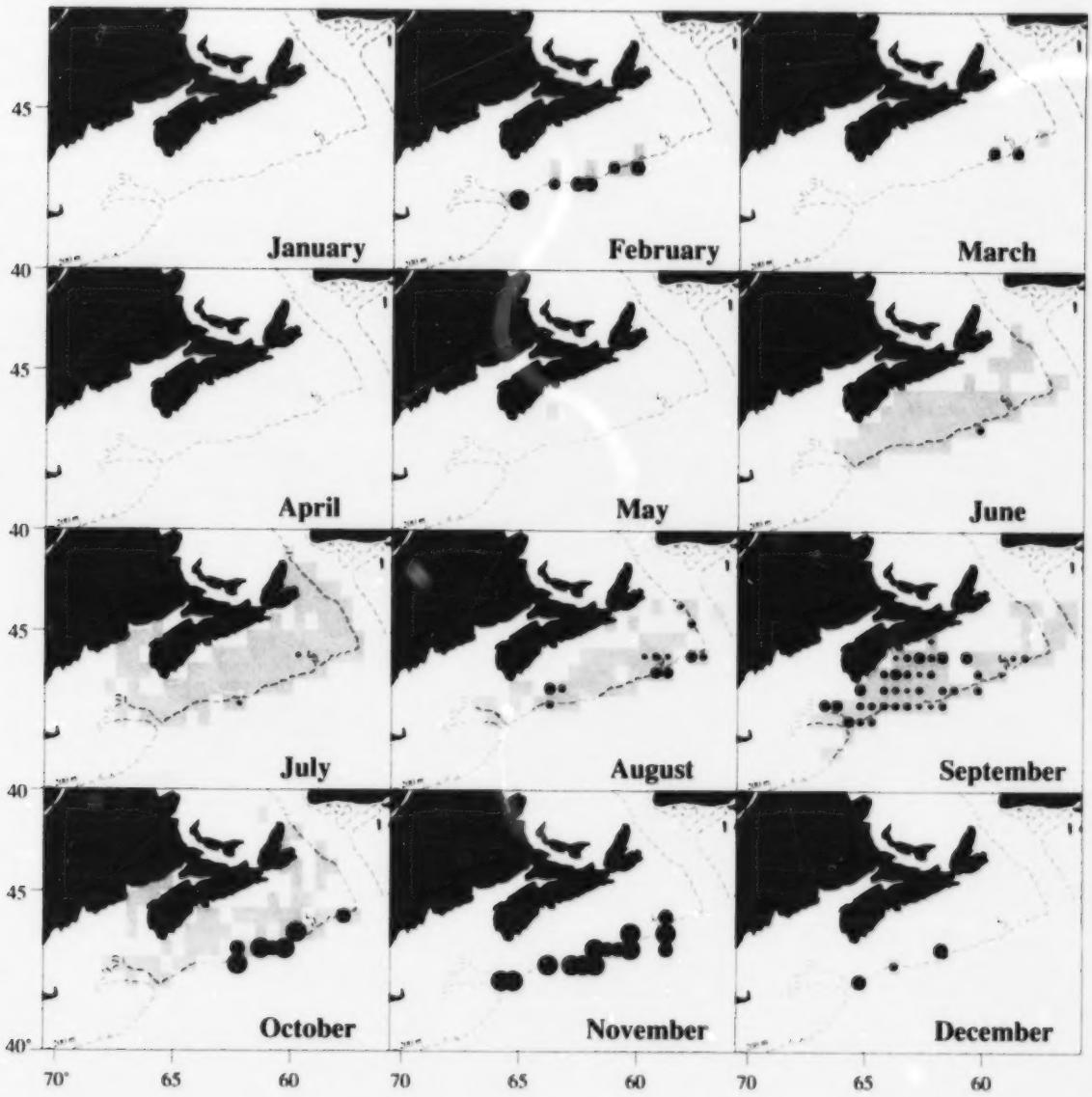


Figure 13 cont. Monthly pattern of distribution over the Scotian Shelf of mature male *Illex illecebrosus* during the period 1970-83.

Area sampled is indicated by shading, and mean catch in number of animals per tow for each 0.5° square is represented by a solid circle scaled to catch level.

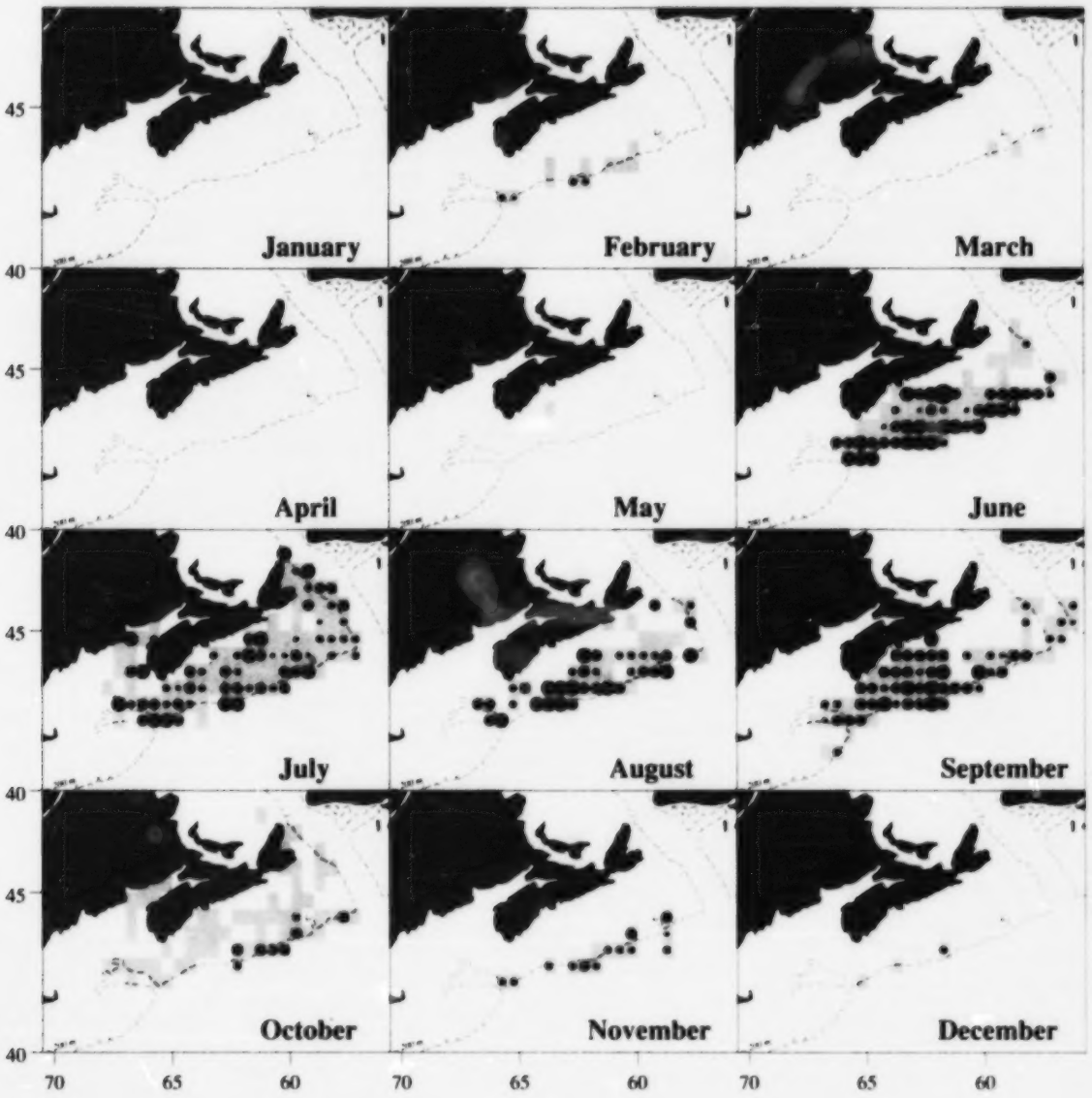


Figure 13 cont. Monthly pattern of distribution over the Scotian Shelf of immature female *Illex illecebrosus* during the period 1970-83.

Area sampled is indicated by shading, and mean catch in number of animals per tow for each 0.5° square is represented by a solid circle scaled to catch level.

Note: "immature female" includes females with a nidamental gland length / mantle length *ratio* < 0.1 (*see* Durward et al., 1979).

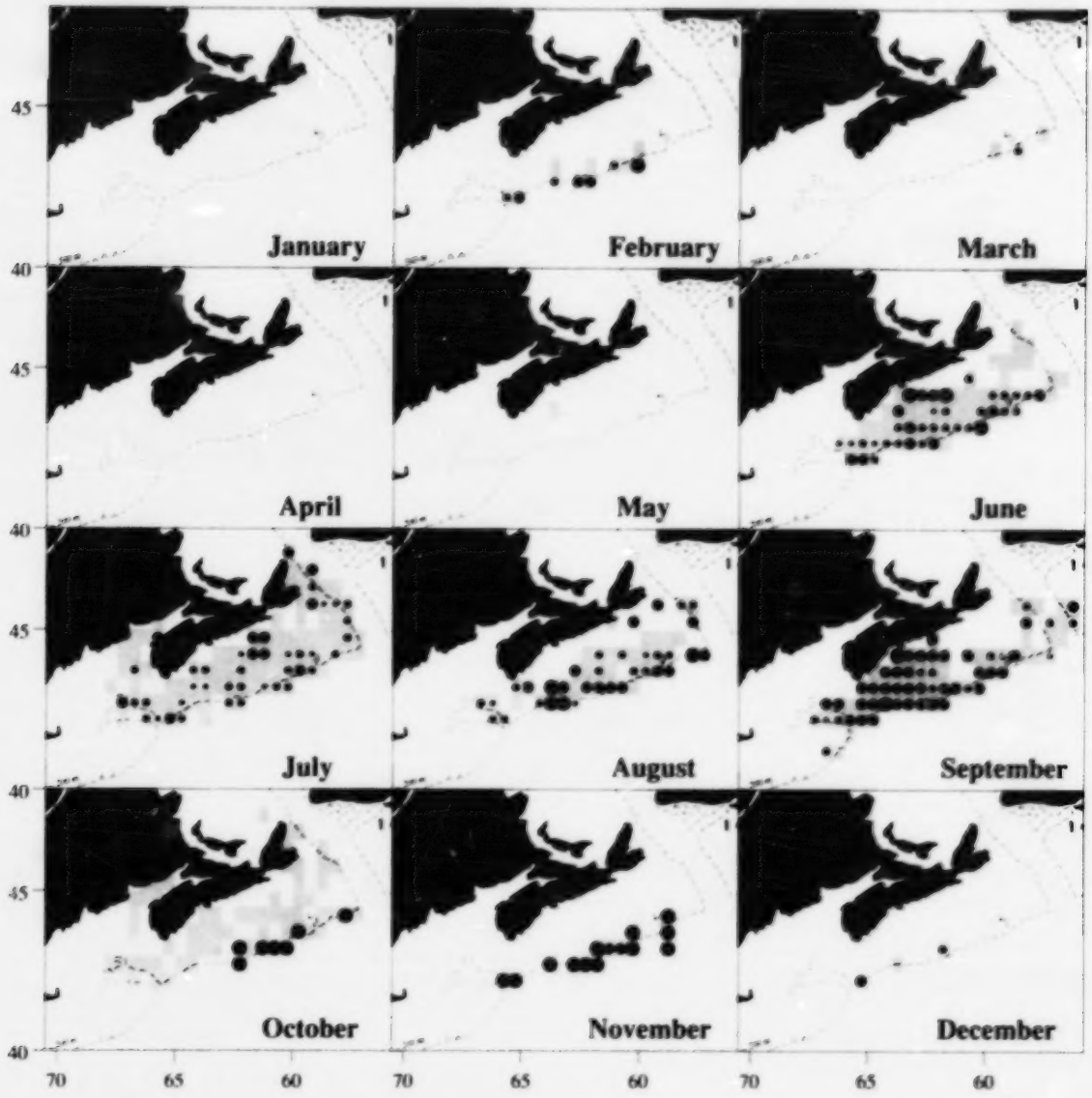


Figure 13 cont. Monthly pattern of distribution over the Scotian Shelf of incipient maturing female *Illex illecebrosus* during the period 1970-83.

Area sampled is indicated by shading, and mean catch in number of animals per tow for each 0.5° square is represented by a solid circle scaled to catch level.

Note: "incipient maturing female" includes females with a nidamental gland length / mantle length *ratio* between 0.1 and 0.2 (*see* Durward et al., 1979).

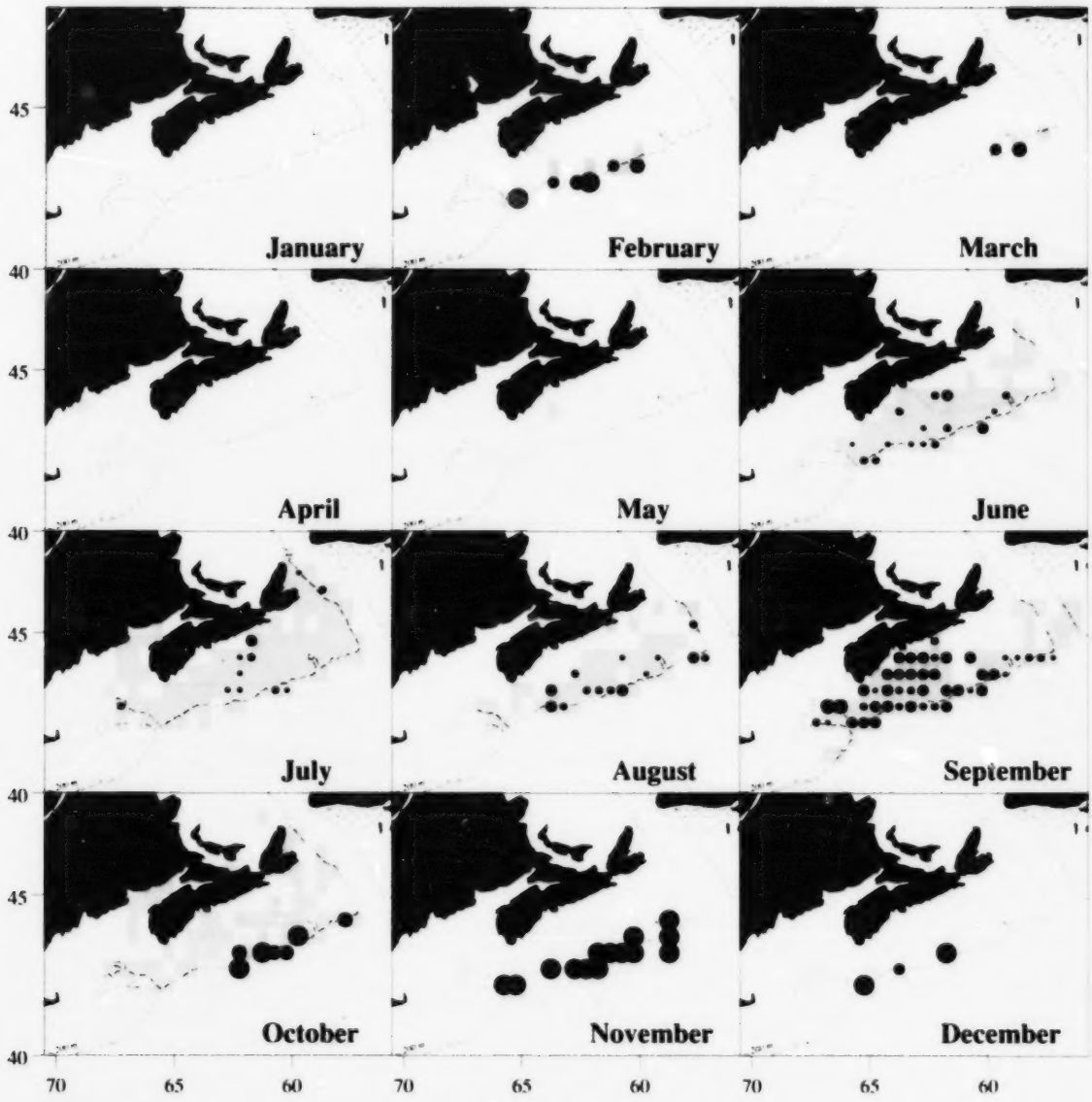


Figure 13 cont. Monthly pattern of distribution over the Scotian Shelf of advanced maturing female *Illex illecebrosus* during the period 1970-83.

Area sampled is indicated by shading, and mean catch in number of animals per tow for each 0.5° square is represented by a solid circle scaled to catch level.

Note: "advanced maturing female" includes females with a nidamental gland length / mantle length *ratio* between 0.2 and 0.35 (*see* Durward et al., 1979).

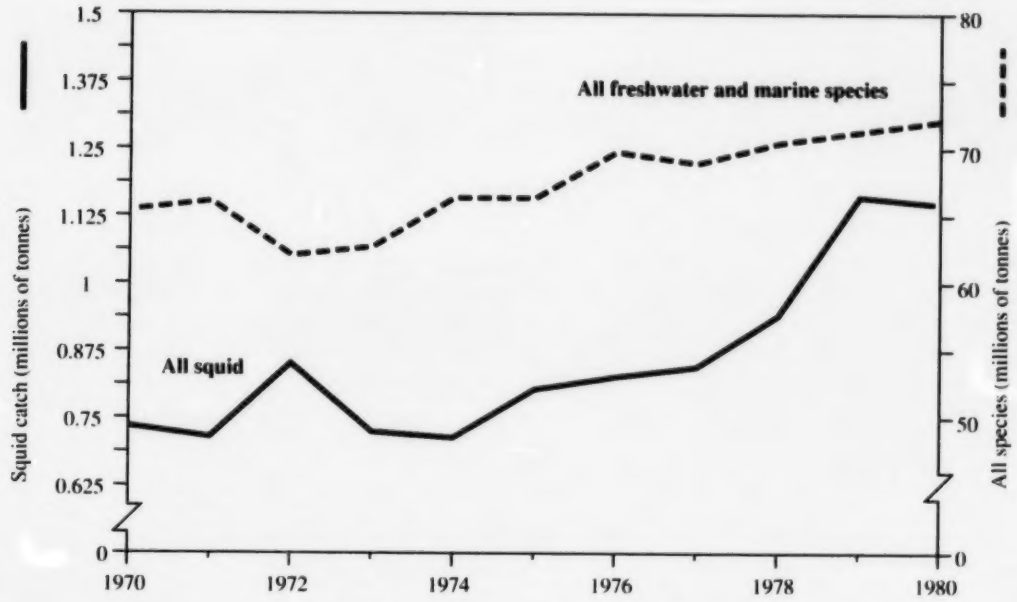


Figure 14. Nominal world catches of squid and nominal world catches of all fish and shellfish in marine and freshwater in millions of tonnes. Source: Worms (1983).

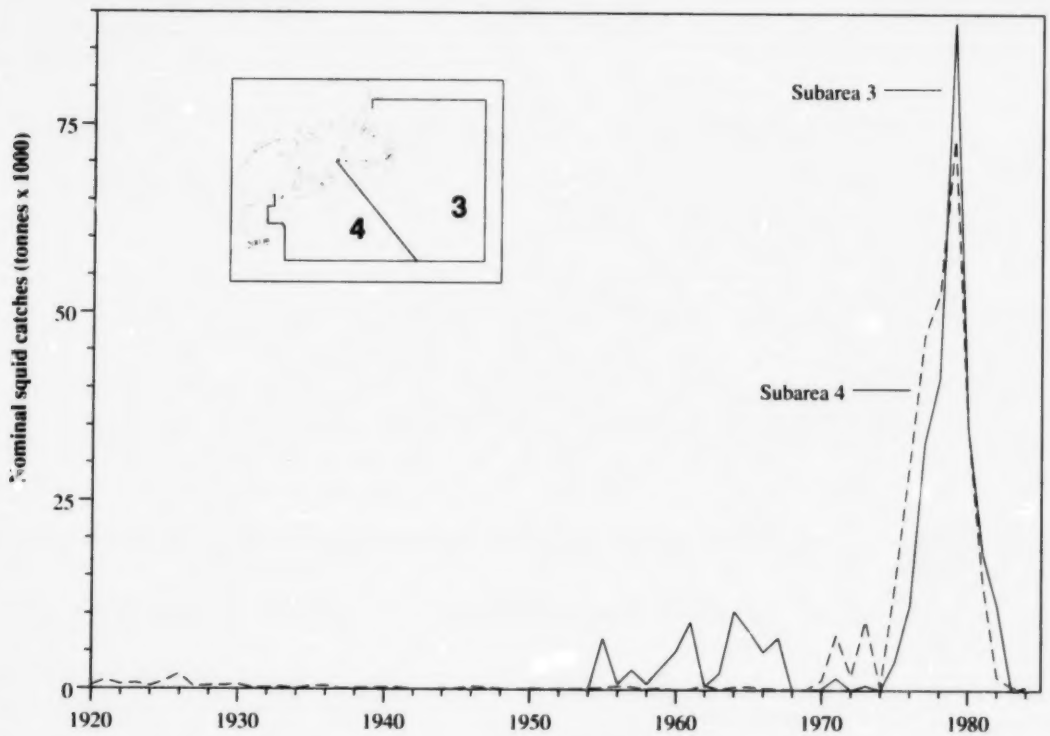


Figure 15. Nominal catches (thousands of tonnes) of *Illex illecebrosus* from Canadian waters for the period 1920-84. Subarea 3 catches prior to 1955 are unavailable. Although breakdown by species is not given prior to 1967, it is highly unlikely that species other than *Illex illecebrosus* contributed significantly to the catch. Source: Northwest Atl. Fish. Organ.Sci. Counc. Rep. 1980, 1985.)

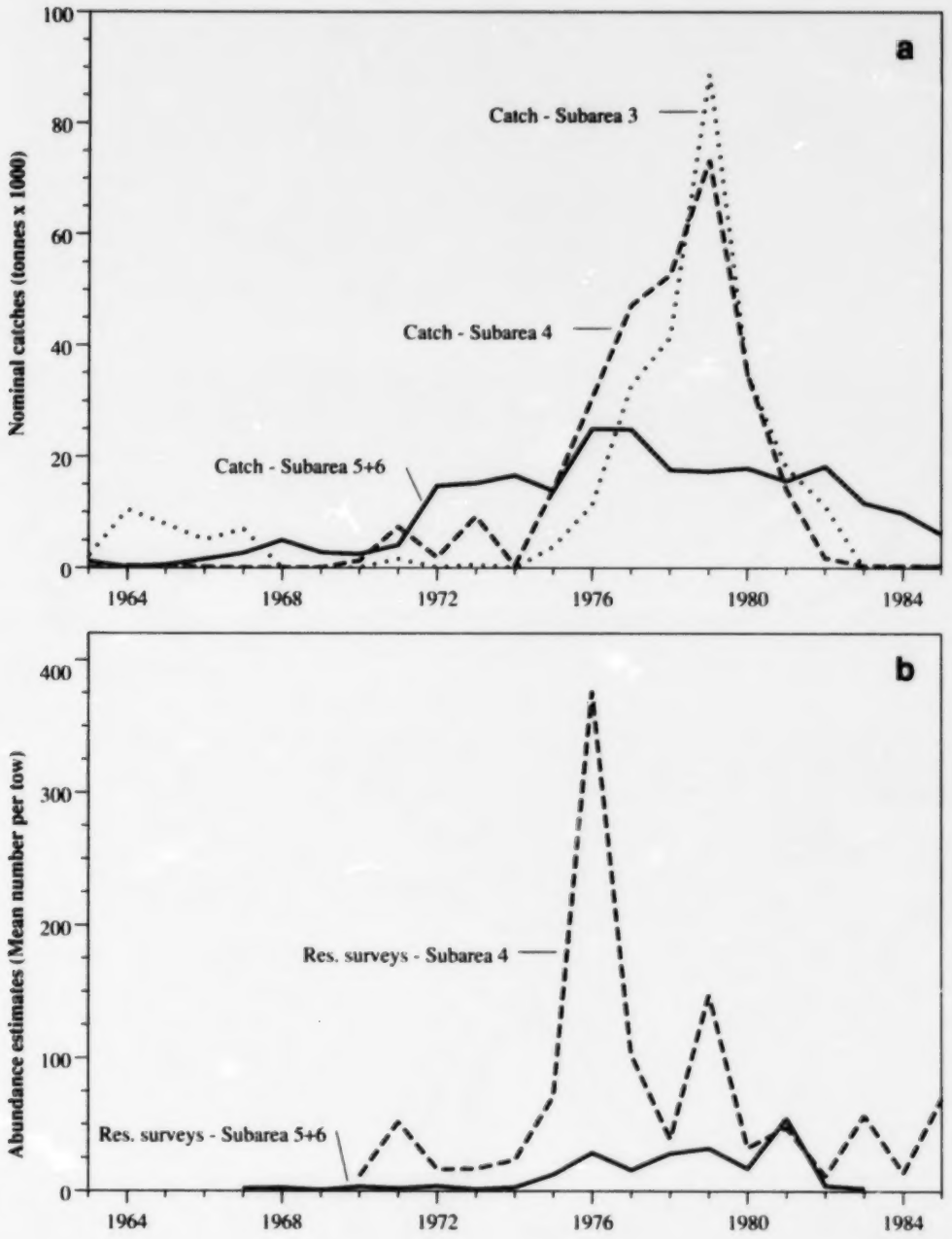


Figure 16. **a** Nominal catches (tonnes) of short-finned squid (*Illex illecebrosus*) in the Northwest Atlantic from 1963 to 1985;
b Research survey abundance estimates (mean number per tow) from Canadian and U.S.A. research surveys for the period 1967-85. Source: Northwest Atl. Fish. Organ. Sci. Counc. Rep. 1980, 1986.

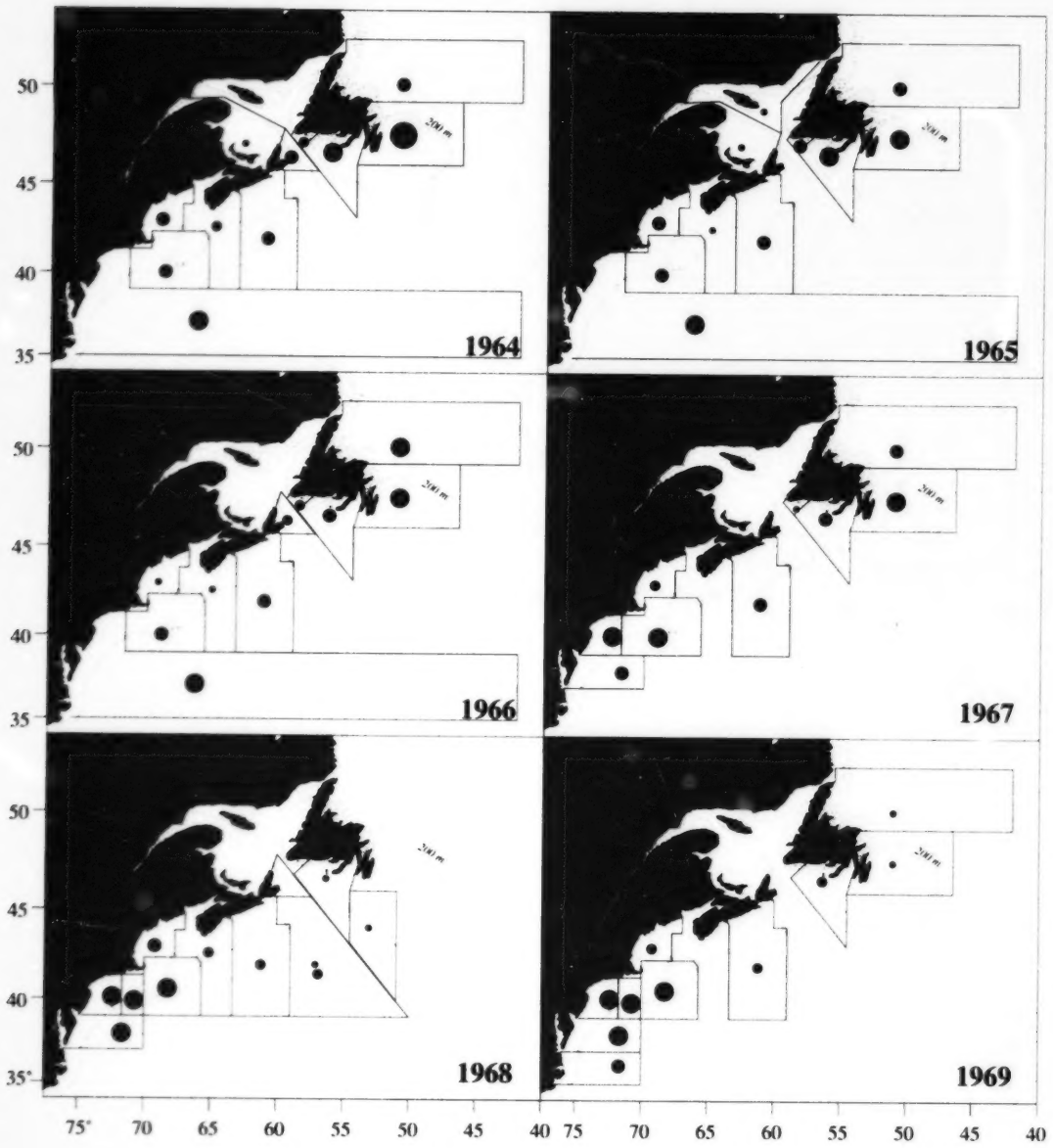


Figure 17. Nominal catches (tonnes) of squids (*Illex* and *Loligo*) by NAFO Subareas and Division for the years 1964 through 1984. Catches from Subareas 3 & 4 are almost entirely *Illex illecebrosus*, while those from Subareas 5 & 6 represent a mixture of *Illex illecebrosus* and *Loligo pealei*. Catch levels (total nominal catch) for each Division (or Subarea) is represented by a solid circle scaled to catch level.

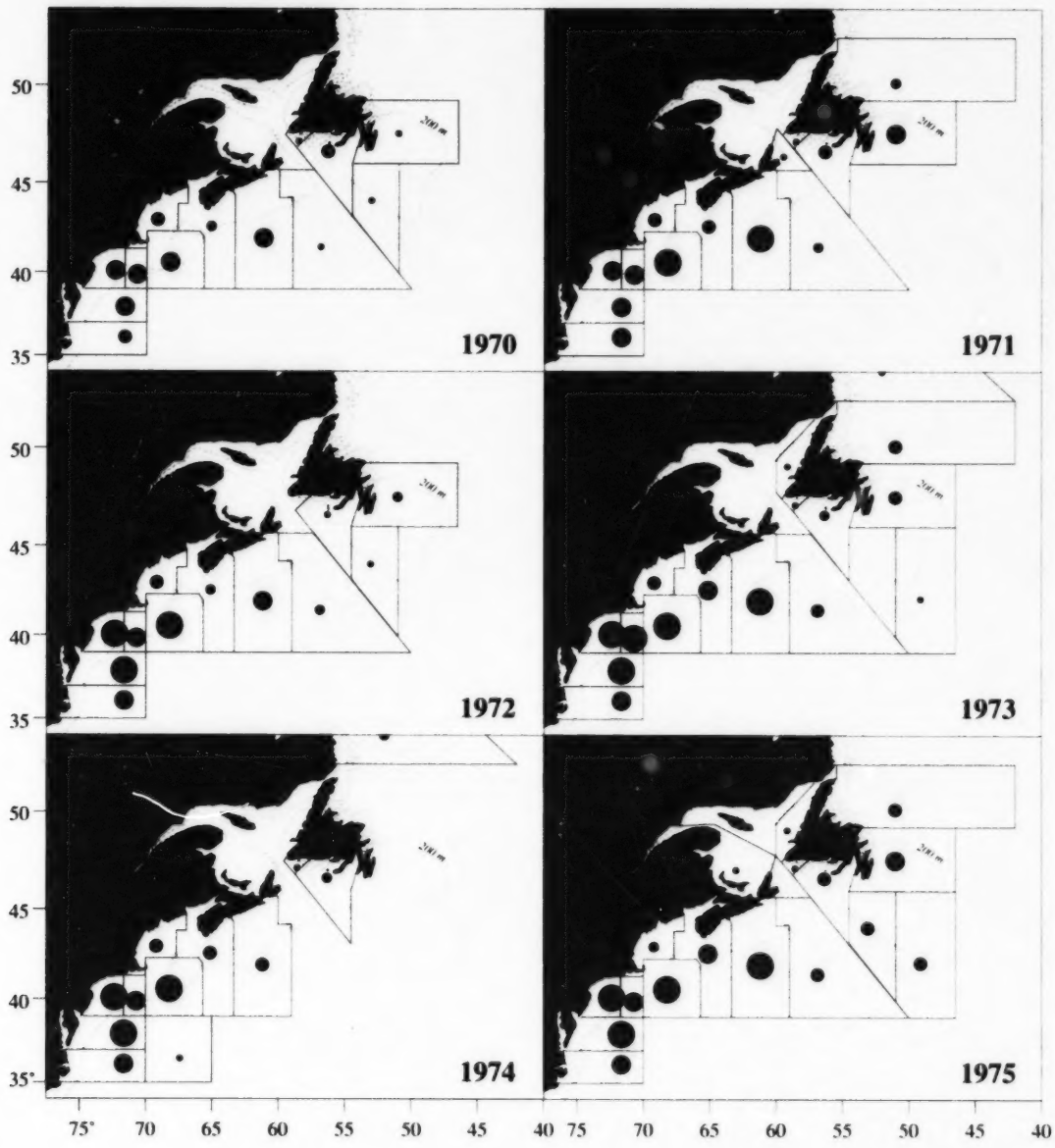


Figure 17 cont. Nominal catches (tonnes) of squids (*Illex* and *Loligo*) by NAFO Subareas and Division for the years 1964 through 1984. Catches from Subareas 3 & 4 are almost entirely *Illex illecebrosus*, while those from Subareas 5 & 6 represent a mixture of *Illex illecebrosus* and *Loligo pealei*. Catch levels (total nominal catch) for each Division (or Subarea) is represented by a solid circle scaled to catch level.

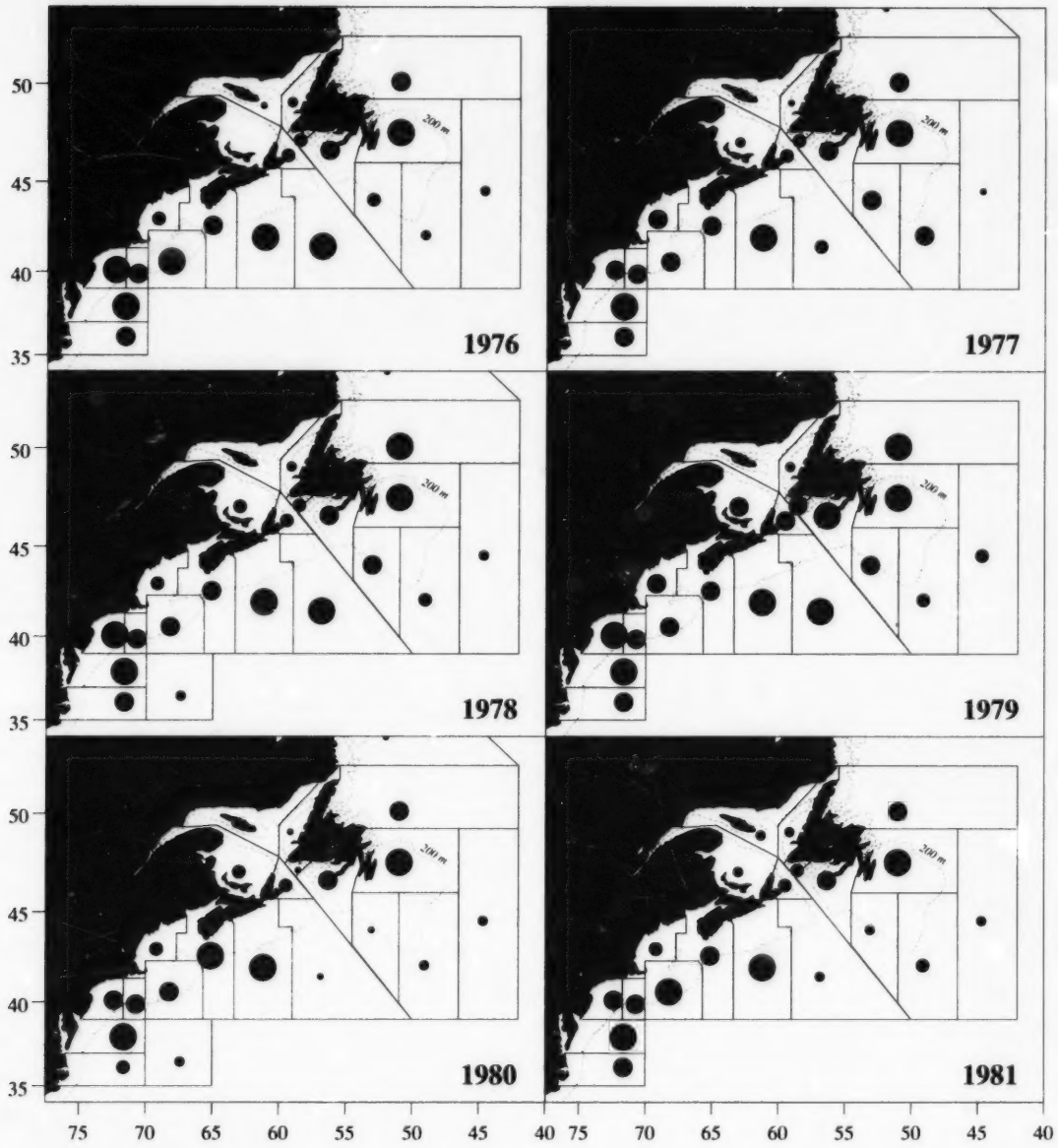


Figure 17 cont. Nominal catches (tonnes) of squids (*Illex* and *Loligo*) by NAFO Subareas and Division for the years 1964 through 1984. Catches from Subareas 3 & 4 are almost entirely *Illex illecebrosus*, while those from Subareas 5 & 6 represent a mixture of *Illex illecebrosus* and *Loligo pealei*. Catch levels (total nominal catch) for each Division (or Subarea) is represented by a solid circle scaled to catch level.

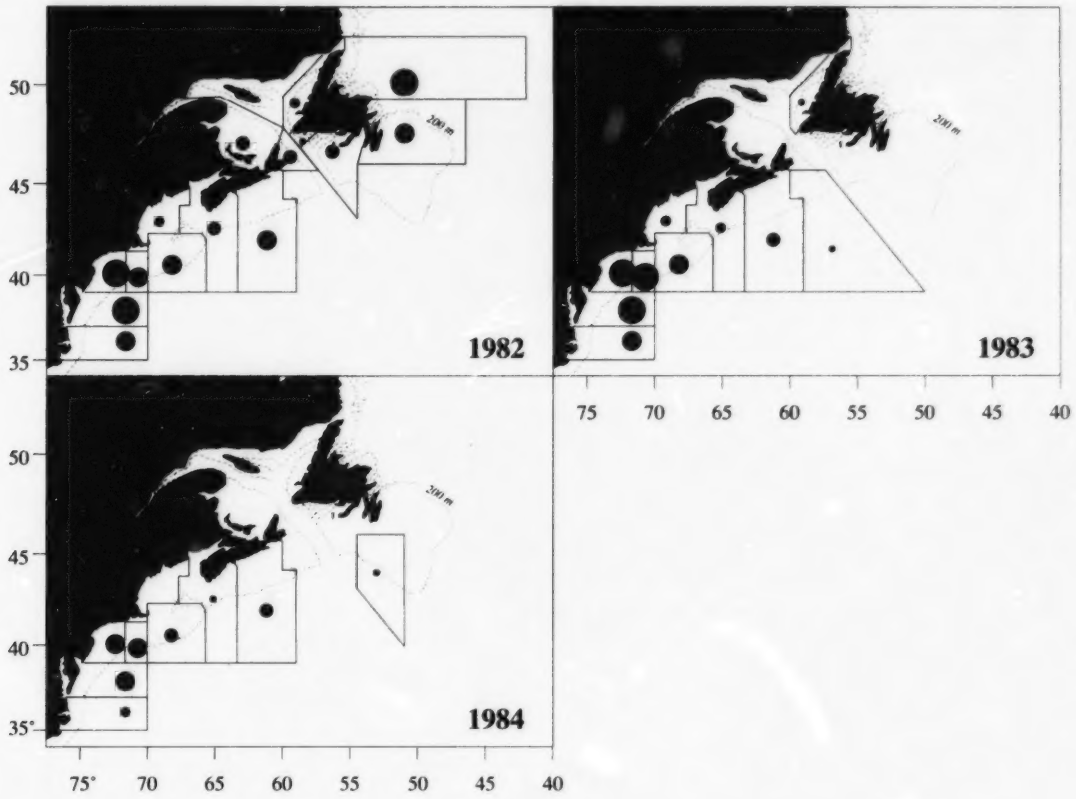
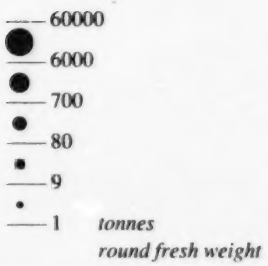


Figure 17 cont. Nominal catches (tonnes) of squids (*Illex* and *Loligo*) by NAFO Subareas and Division for the years 1964 through 1984. Catches from Subareas 3 & 4 are almost entirely *Illex illecebrosus*, while those from Subareas 5 & 6 represent a mixture of *Illex illecebrosus* and *Loligo pealei*. Catch levels (total nominal catch) for each Division (or Subarea) is represented by a solid circle scaled to catch level.



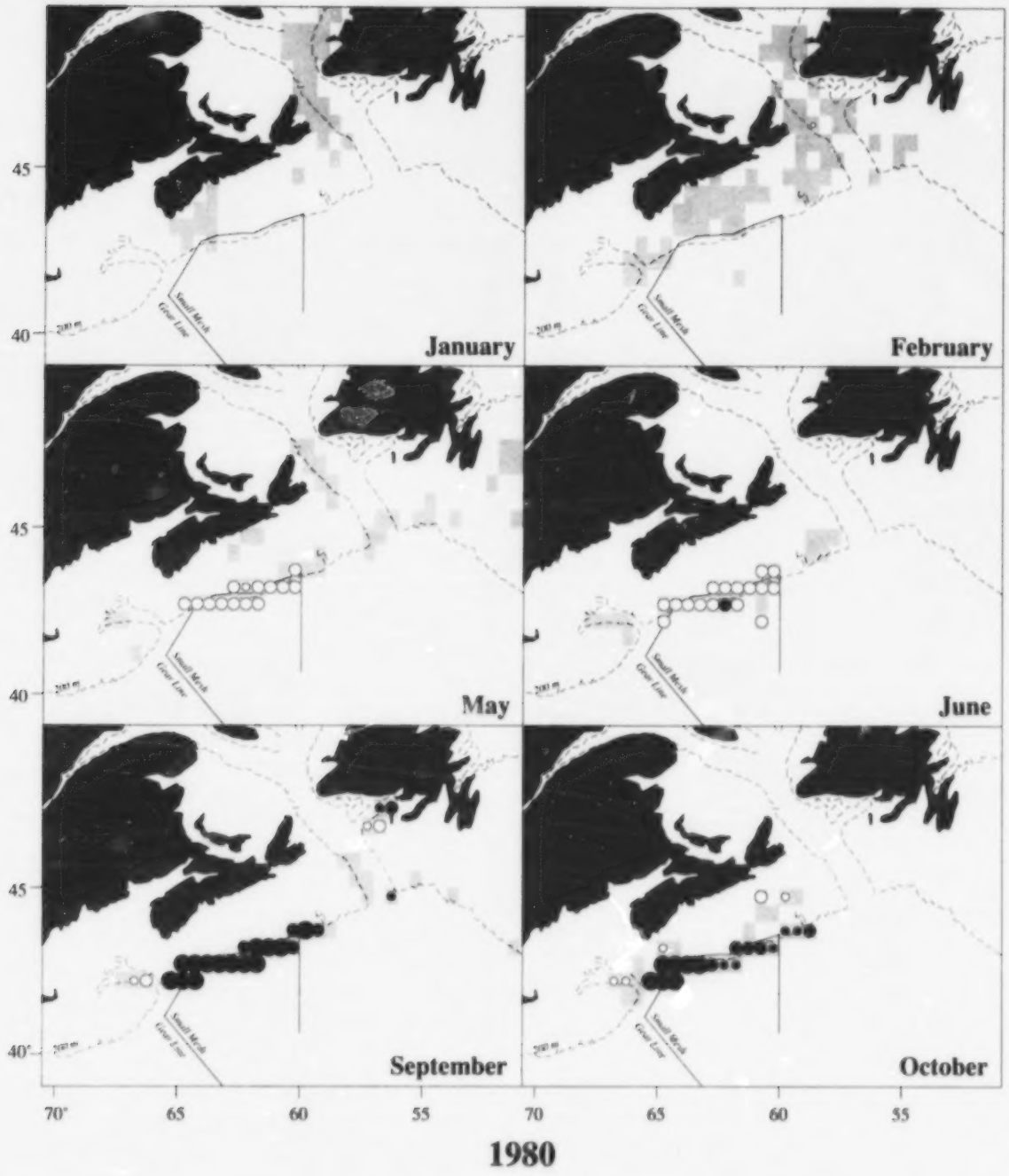


Figure 18. Monthly distribution of commercial catches of *Illex illecebrosus* by foreign fleets in Canadian waters as determined from International Observer Program sampling for the years 1980 through 1985.

Areas sampled are indicated by shading. Catches in kg/hour per 0.5° square are represented by circles scaled to catch level. Open circles are used for squares where all sets (tows) caught *Illex* only as a bycatch. Solid circles are used for squares where one or more sets caught squid as a "directed catch" (i.e. greater than 50% by weight).

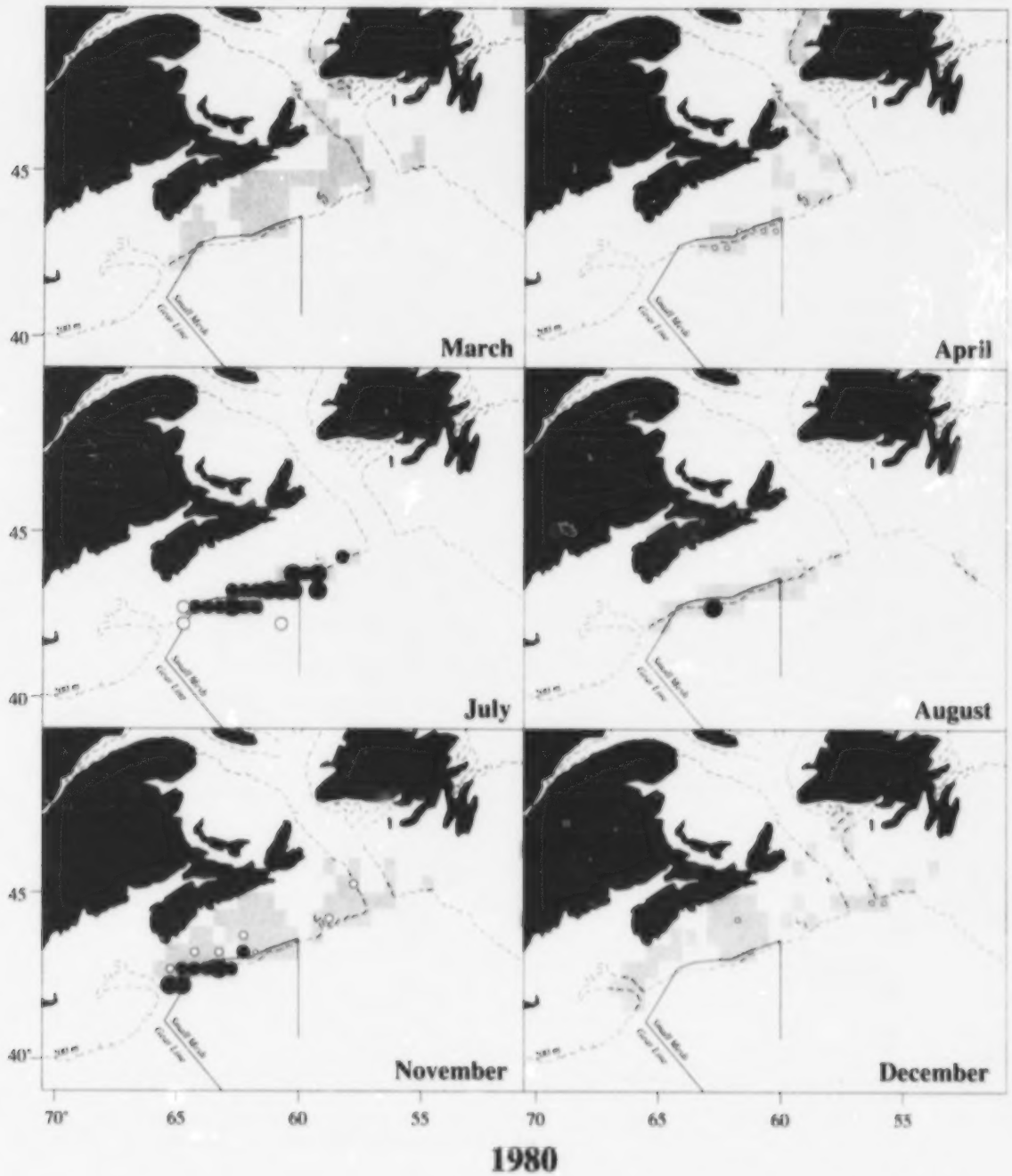


Figure 18 cont. Monthly distribution of commercial catches of *Illex illecebrosus* by foreign fleets in Canadian waters as determined from International Observer Program sampling for the years 1980 through 1985.

Areas sampled are indicated by shading. Catches in kg/hour per 0.5° square are represented by circles scaled to catch level. Open circles are used for squares where all sets (tows) caught *Illex* only as a bycatch. Solid circles are used for squares where one or more sets caught squid as a "directed catch" (i.e. greater than 50% by weight).

7000
400
20
1
0.1 *kg/hour*

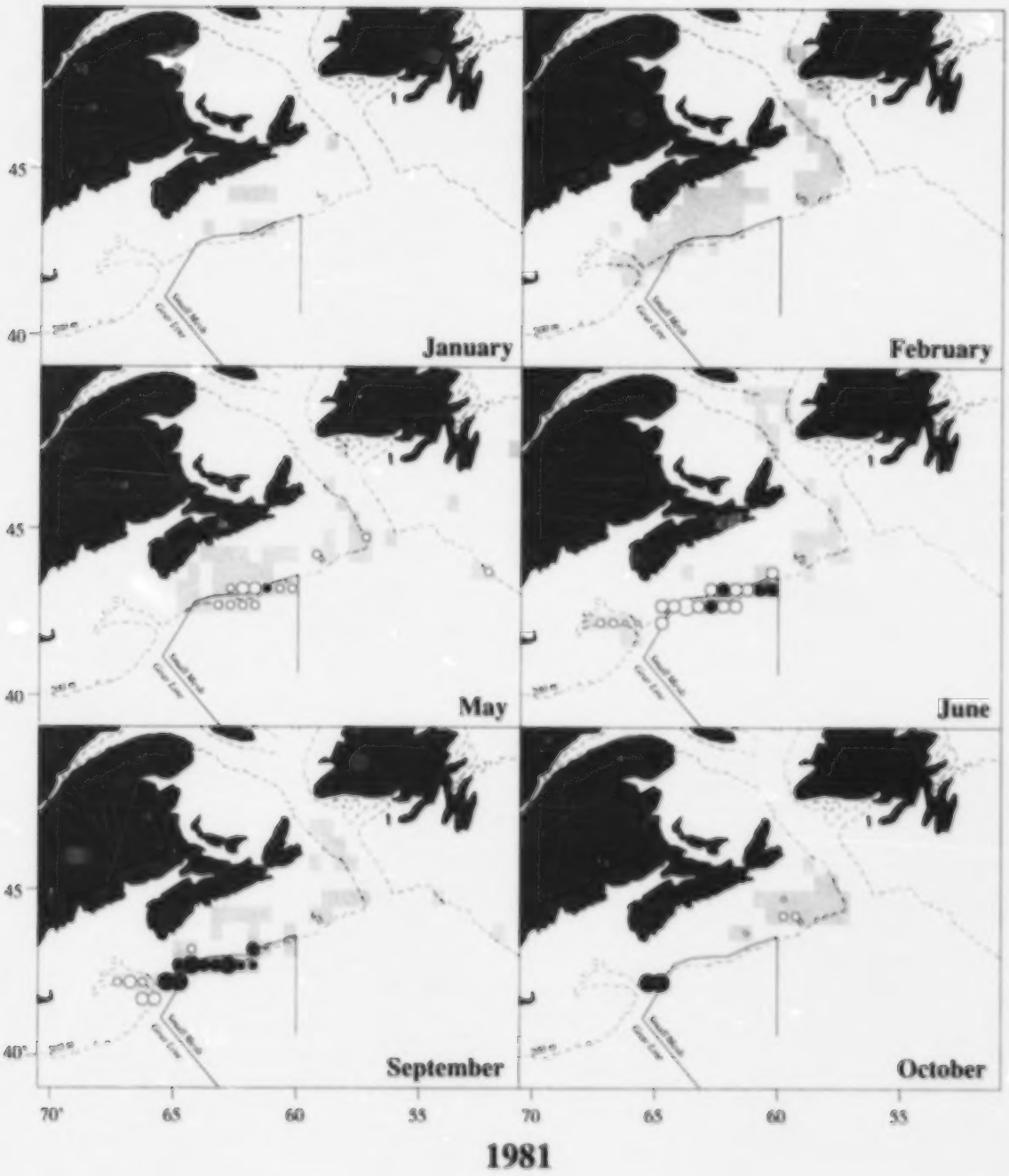


Figure 18 cont. Monthly distribution of commercial catches of *Illex illecebrosus* by foreign fleets in Canadian waters as determined from International Observer Program sampling for the years 1980 through 1985.

Areas sampled are indicated by shading. Catches in kg/hour per 0.5° square are represented by circles scaled to catch level. Open circles are used for squares where all sets (tows) caught *Illex* only as a bycatch. Solid circles are used for squares where one or more sets caught squid as a "directed catch" (i.e. greater than 50% by weight).

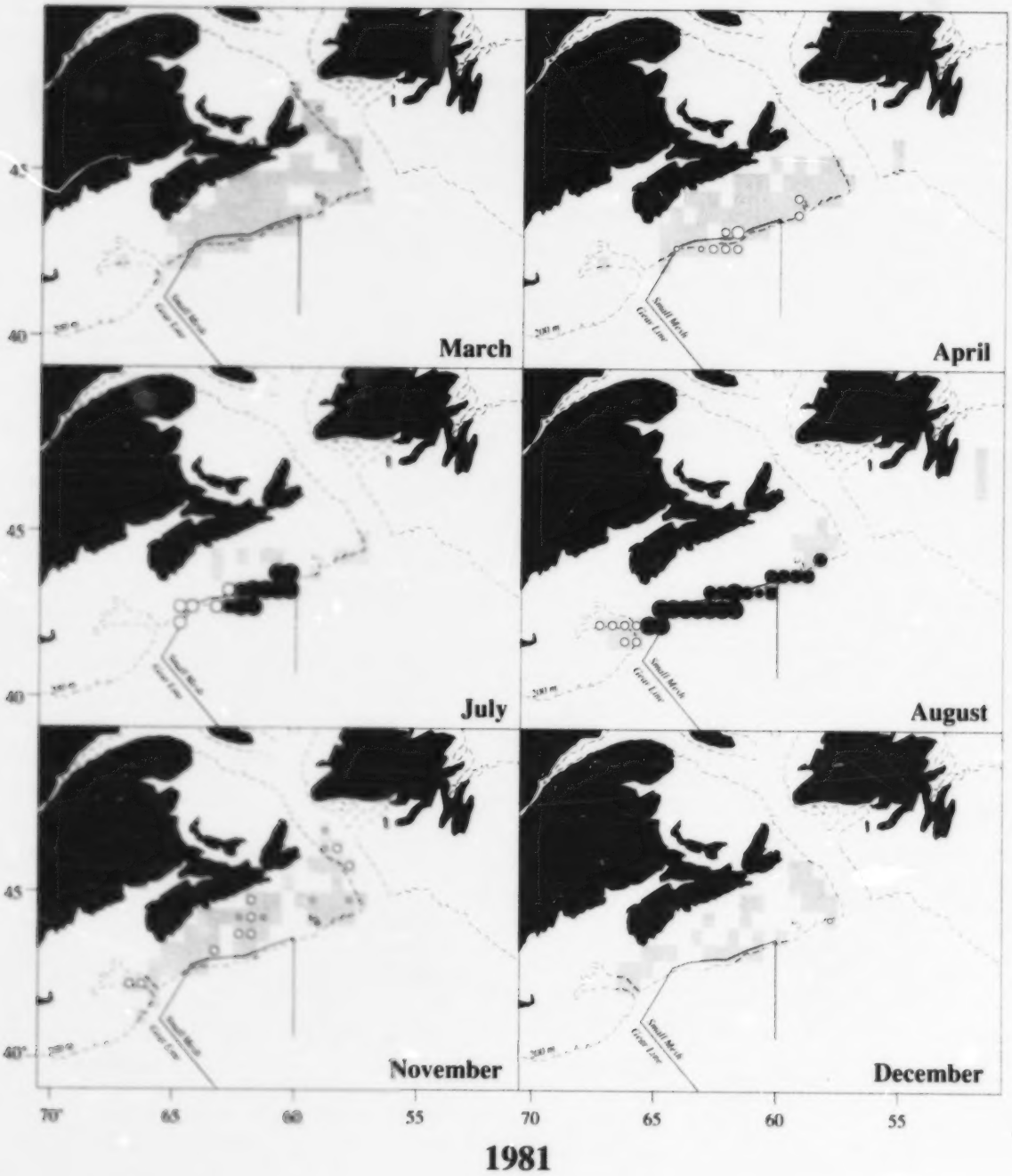


Figure 18 cont. Monthly distribution of commercial catches of *Illex illecebrosus* by foreign fleets in Canadian waters as determined from International Observer Program sampling for the years 1980 through 1985.

Areas sampled are indicated by shading. Catches in kg/hour per 0.5° square are represented by circles scaled to catch level. Open circles are used for squares where all sets (tows) caught *Illex* only as a bycatch. Solid circles are used for squares where one or more sets caught squid as a "directed catch" (i.e. greater than 50% by weight).

7000
400
20
1
0.1 *kg/hour*

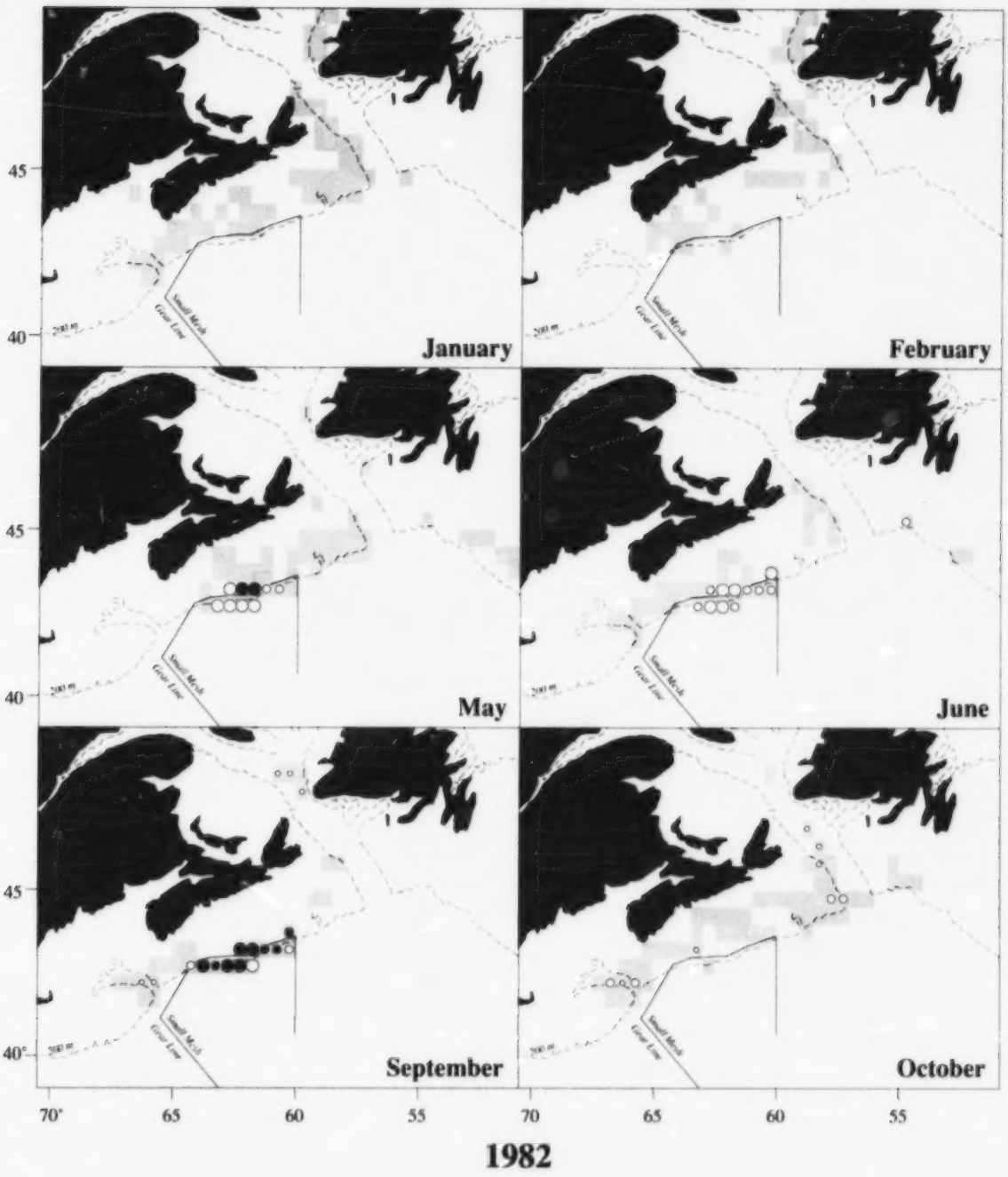


Figure 18 cont. Monthly distribution of commercial catches of *Illex illecebrosus* by foreign fleets in Canadian waters as determined from International Observer Program sampling for the years 1980 through 1985.

Areas sampled are indicated by shading. Catches in kg/hour per 0.5° square are represented by circles scaled to catch level. Open circles are used for squares where all sets (tows) caught *Illex* only as a bycatch. Solid circles are used for squares where one or more sets caught squid as a "directed catch" (i.e. greater than 50% by weight).

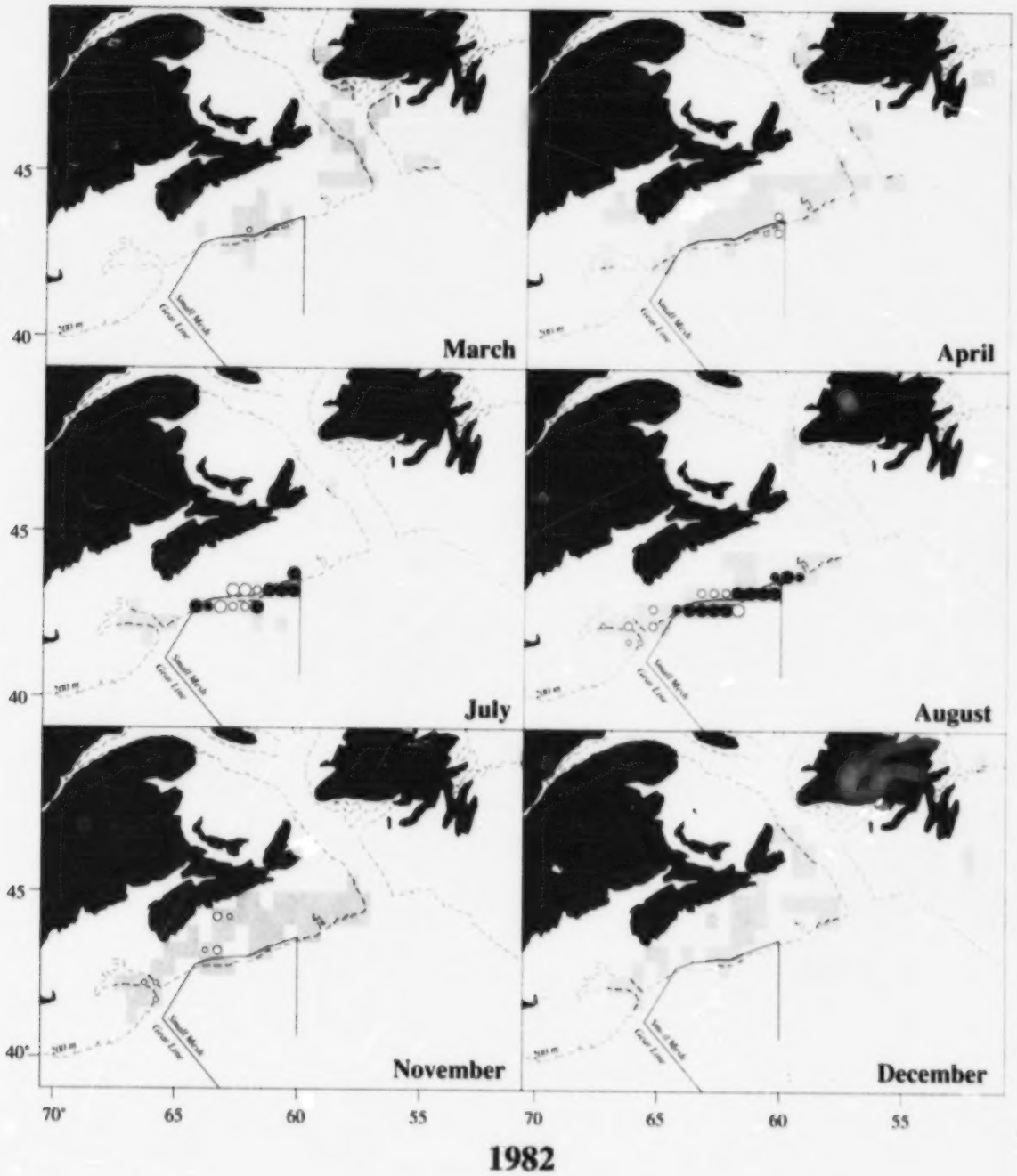


Figure 18 cont. Monthly distribution of commercial catches of *Illex illecebrosus* by foreign fleets in Canadian waters as determined from International Observer Program sampling for the years 1980 through 1985.

Areas sampled are indicated by shading. Catches in kg/hour per 0.5° square are represented by circles scaled to catch level. Open circles are used for squares where all sets (tows) caught *Illex* only as a bycatch. Solid circles are used for squares where one or more sets caught squid as a "directed catch" (i.e. greater than 50% by weight).

7000
400
20
1
0.1 *kg/hour*

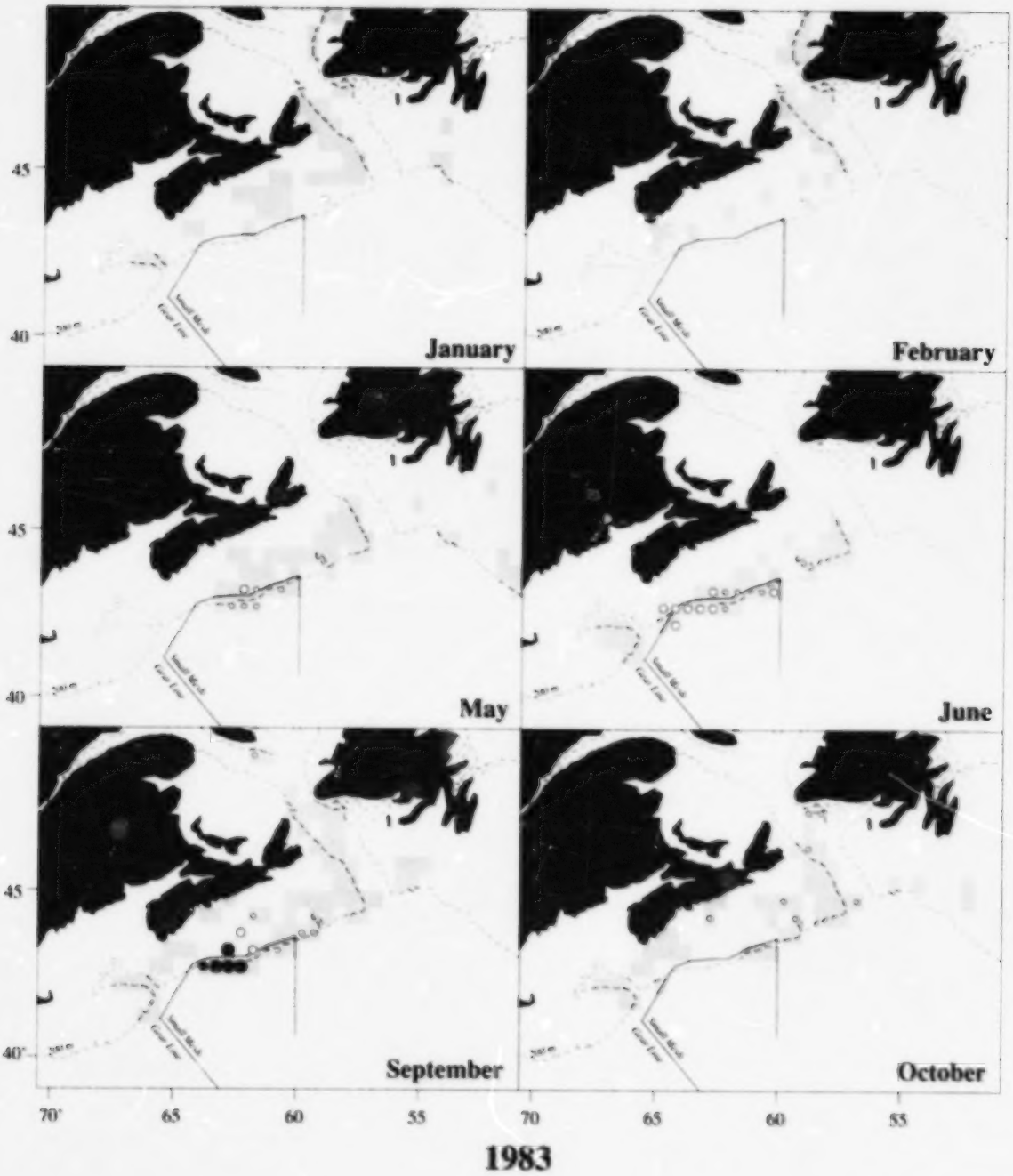


Figure 18 cont. Monthly distribution of commercial catches of *Illex illecebrosus* by foreign fleets in Canadian waters as determined from International Observer Program sampling for the years 1980 through 1985.

Areas sampled are indicated by shading. Catches in kg/hour per 0.5° square are represented by circles scaled to catch level. Open circles are used for squares where all sets (tows) caught *Illex* only as a bycatch. Solid circles are used for squares where one or more sets caught squid as a "directed catch" (i.e. greater than 50% by weight).

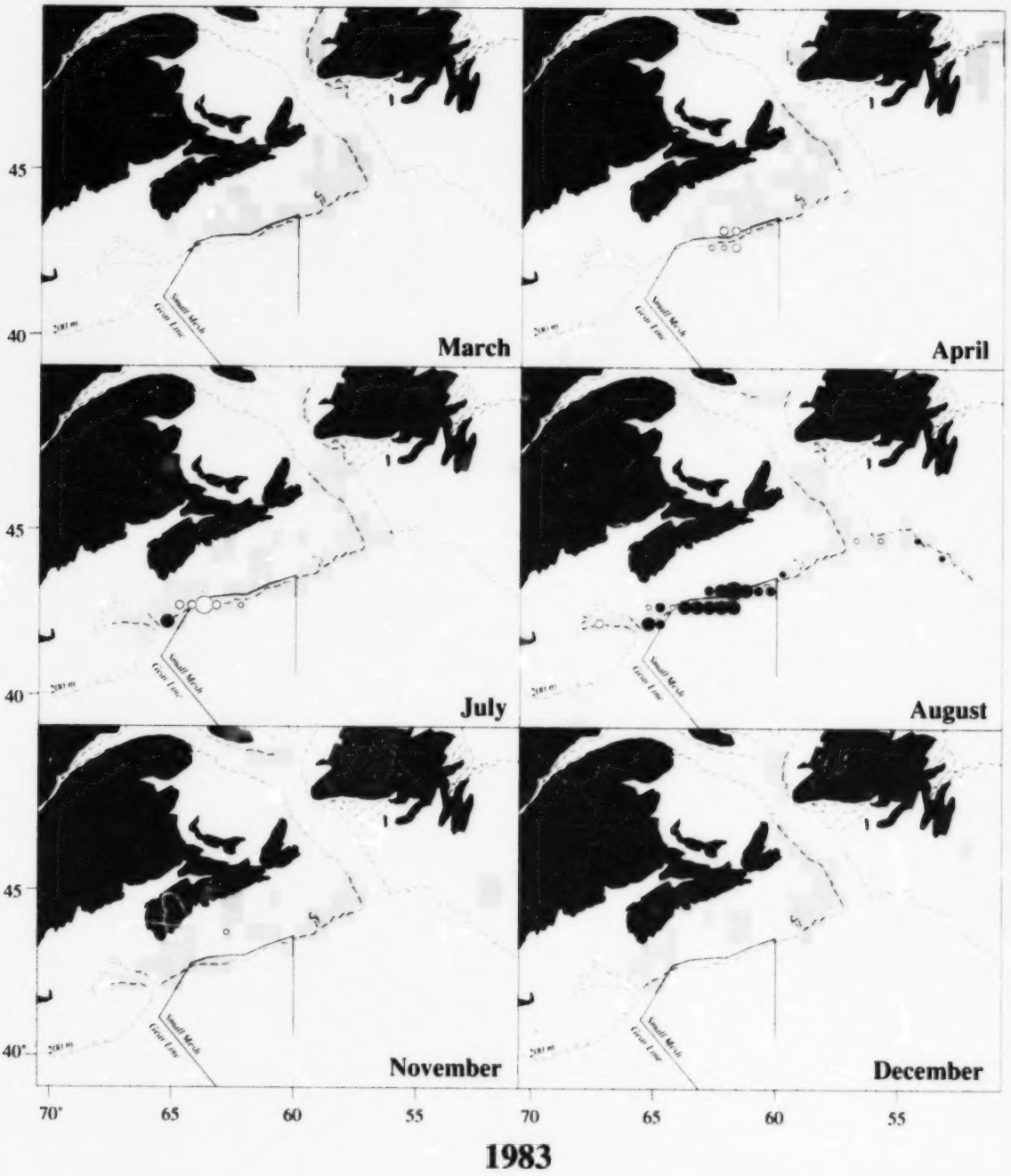


Figure 18 cont. Monthly distribution of commercial catches of *Illex illecebrosus* by foreign fleets in Canadian waters as determined from International Observer Program sampling for the years 1980 through 1985.

Areas sampled are indicated by shading. Catches in kg/hour per 0.5° square are represented by circles scaled to catch level. Open circles are used for squares where all sets (tows) caught *Illex* only as a bycatch. Solid circles are used for squares where one or more sets caught squid as a "directed catch" (i.e. greater than 50% by weight).

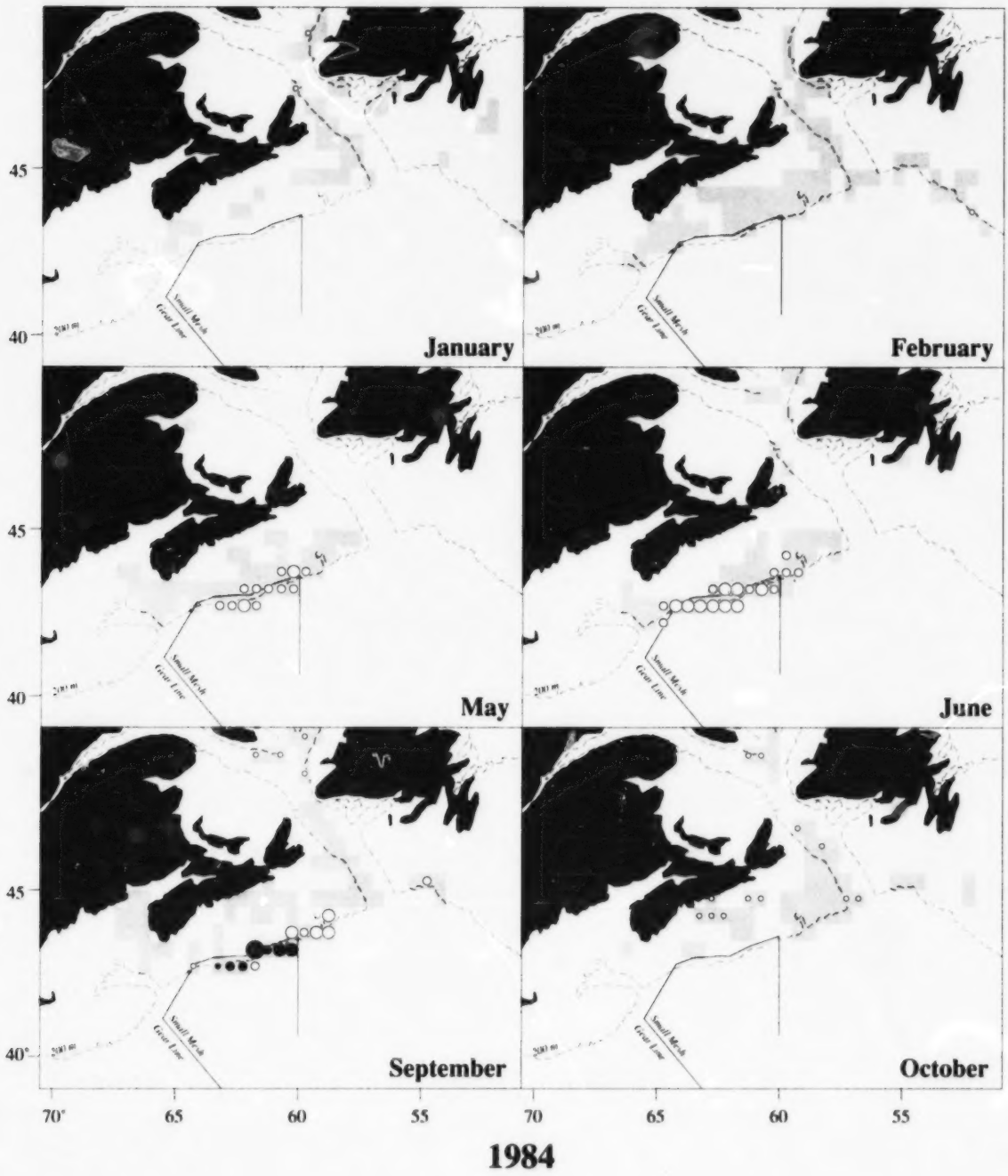


Figure 18 cont. Monthly distribution of commercial catches of *Illex illecebrosus* by foreign fleets in Canadian waters as determined from International Observer Program sampling for the years 1980 through 1985.

Areas sampled are indicated by shading. Catches in kg/hour per 0.5° square are represented by circles scaled to catch level. Open circles are used for squares where all sets (tows) caught *Illex* only as a bycatch. Solid circles are used for squares where one or more sets caught squid as a "directed catch" (i.e. greater than 50% by weight).

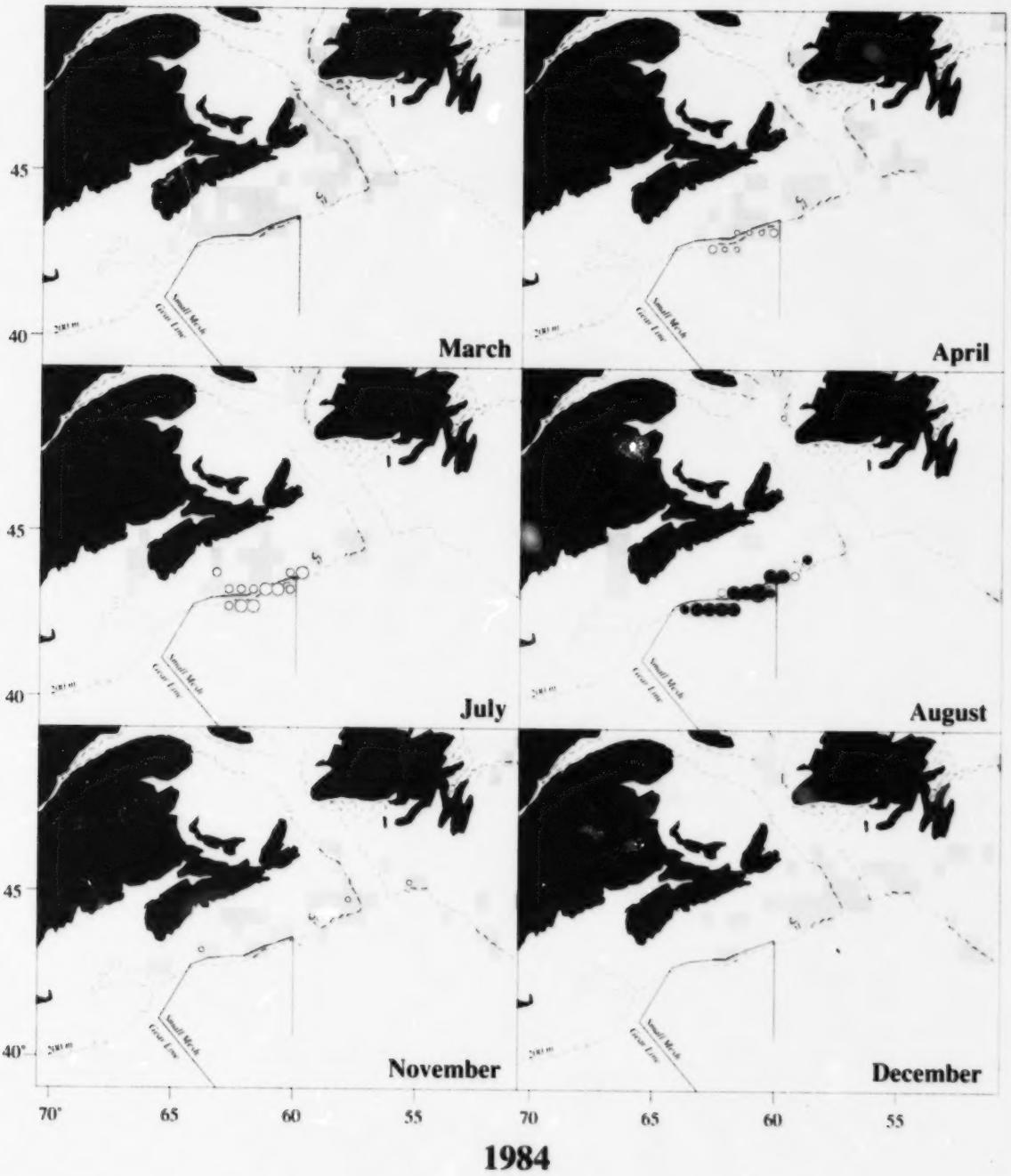


Figure 18 cont. Monthly distribution of commercial catches of *Illex illecebrosus* by foreign fleets in Canadian waters as determined from International Observer Program sampling for the years 1980 through 1985.

Areas sampled are indicated by shading. Catches in kg/hour per 0.5° square are represented by circles scaled to catch level. Open circles are used for squares where all sets (tows) caught *Illex* only as a bycatch. Solid circles are used for squares where one or more sets caught squid as a "directed catch" (i.e. greater than 50% by weight).

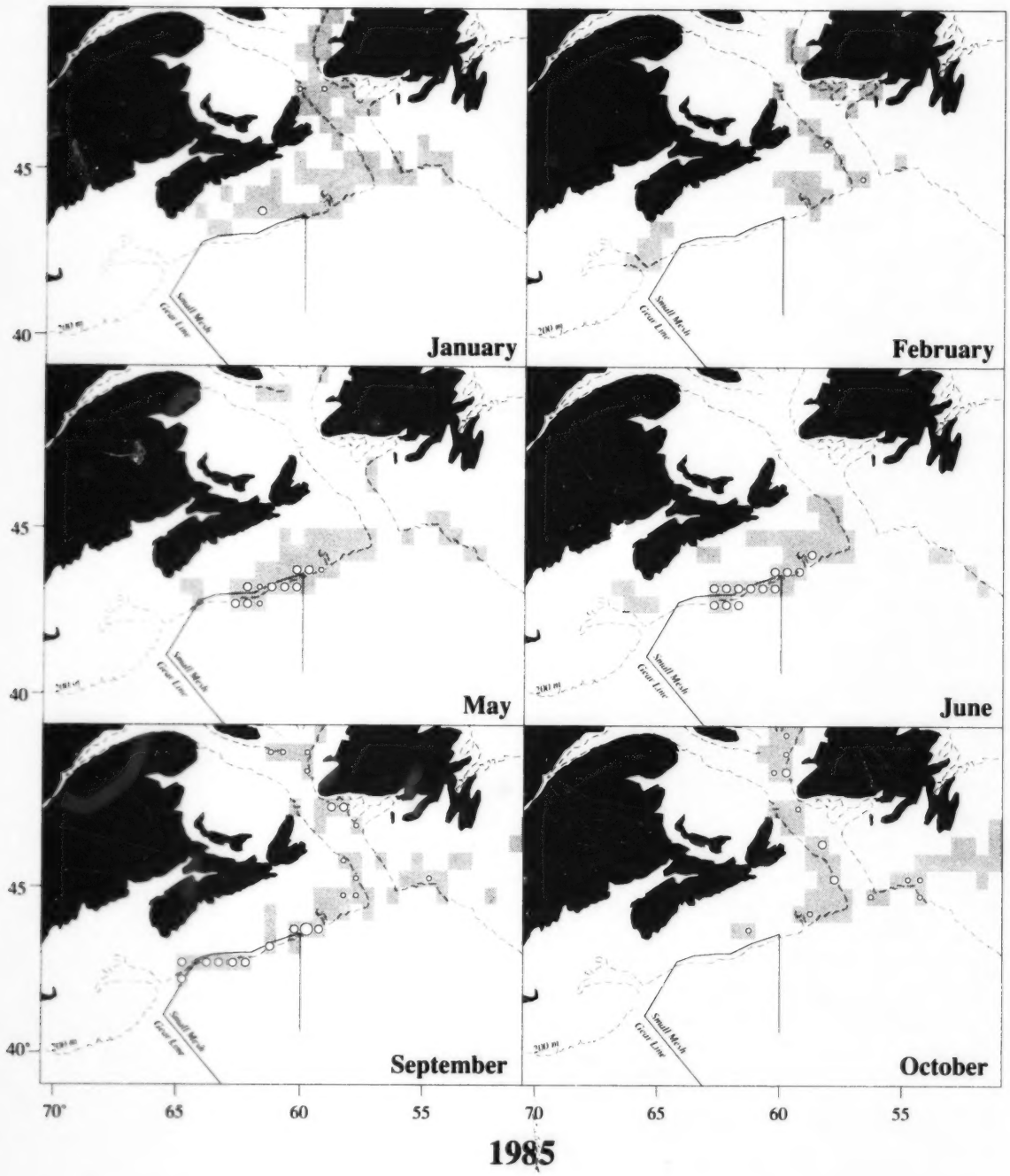


Figure 18 cont. Monthly distribution of commercial catches of *Illex illecebrosus* by foreign fleets in Canadian waters as determined from International Observer Program sampling for the years 1980 through 1985.

Areas sampled are indicated by shading. Catches in kg/hour per 0.5° square are represented by circles scaled to catch level. Open circles are used for squares where all sets (tows) caught *Illex* only as a bycatch. Solid circles are used for squares where one or more sets caught squid as a "directed catch" (i.e. greater than 50% by weight).

Figure 18 cont. Monthly distribution of commercial catches of *Illex illecebrosus* by foreign fleets in Canadian waters as determined from International Observer Program sampling for the years 1980 through 1985.

Areas sampled are indicated by shading. Catches in kg/hour per 0.5° square are represented by circles scaled to catch level. Open circles are used for squares where all sets (tows) caught *Illex* only as a bycatch. Solid circles are used for squares where one or more sets caught squid as a "directed catch" (i.e. greater than 50% by weight).

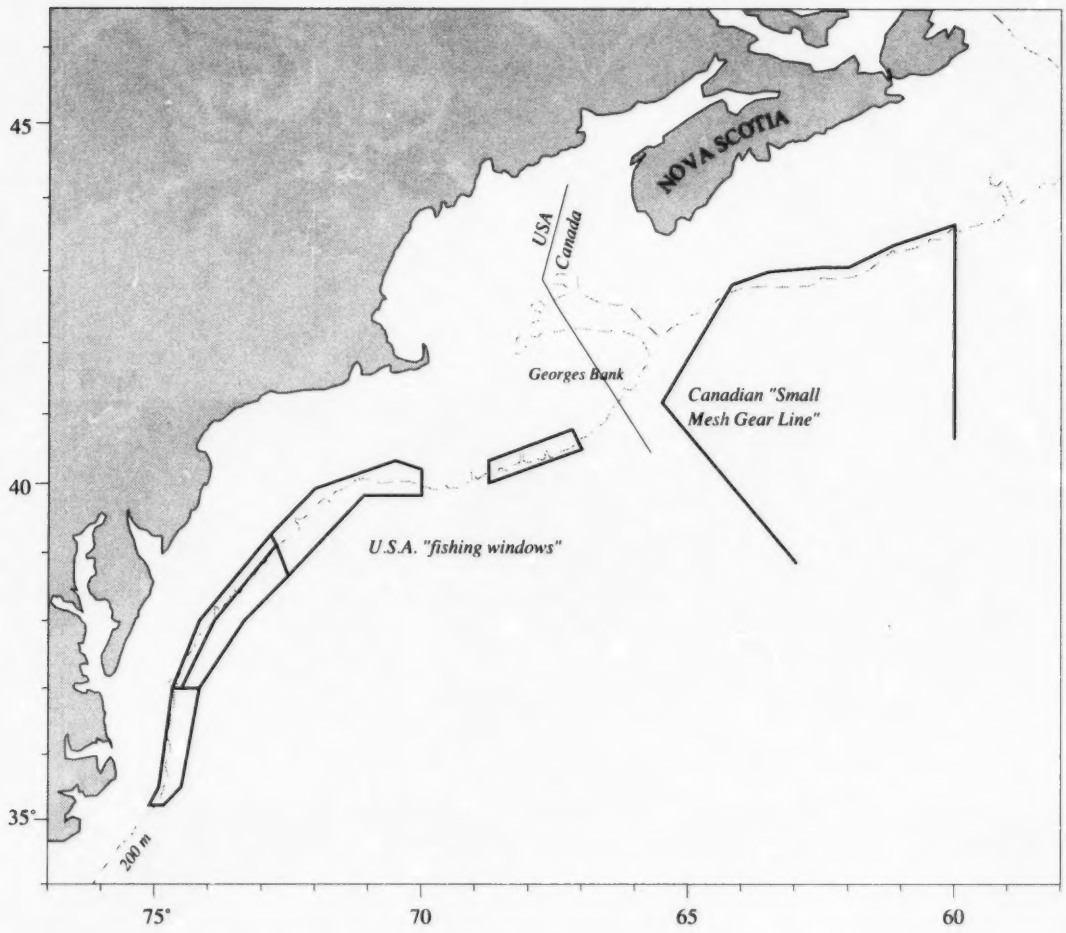


Figure 19. Management areas and boundaries relevant to the squid fisheries (200-mile limit not shown).

References

Anon. 1975. Int. Comm. Northwest Atl. Fish. Redbook. 127 p.

Anon. 1978. Final environmental impact statement/ fishery management plan for the squid fishery of the Northwest Atlantic Ocean. Mid-Atlantic Fishery Management Council. (Room 2115, Federal Building, 300 South New St., Dover, Del. 19901-6790). 91-96.

Anon. 1979-80. Northwest Atl. Fish. Organ. Sci. Coun. Rep. 189 p.

Anon. 1984. Northwest Atl. Fish. Organ. Sci. Coun. Rep. 126 p.

Anon. 1987. Yearbook of fishery statistics. Annuaire statistique des pêches. Annuario estadistico de pesca. 1985 catches and landings. FAO, Rome. Vol 60. 463 p.

Amaratunga, T. 1980. Growth and maturation patterns of the short-finned squid (*Illex illecebrosus*) on the Scotian Shelf. Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 80(II/30): 17 p.

Amaratunga, T. 1983. The role of cephalopods in the marine ecosystem. *in* Advances in assessment of world cephalopod resources. Progrès réalises dans l'évaluation des ressources mondiales de céphalopodes. Progresos realizados en la evaluación mundial de cefalópodos. J. F. Caddy (ed.). FAO Fish. Tech. Pap./FAO, Doc. Tech. Pêches/FAO, Doc. Tec. Pesca 231: 379-415.

Amaratunga, T., and R.D. Durward. 1979. Standardization of data collection for the short-finned squid, *Illex illecebrosus*. Int. Comm. Northwest Atl. Fish. Sel. Pap. No. 5: 37-41.

Amaratunga, T., J.D. Neilson, D.J. Gillis, and L.G. Valdron. 1979. Food and feeding of the short-finned squid, *Illex illecebrosus*, on the Scotian Shelf in 1978. Int. Comm. Northwest Atl. Fish. Res. Doc. 79(II/11): 24 p.

Amaratunga, T., T. Rowell, and M. Roberge. 1980. Summary of joint Canada/U.S.S.R. research program on short-finned squid (*Illex illecebrosus*), 16 February to 4 June 1979: spawning stock and larval survey. Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 80(II/38): 36 p.

Arnold, J.M., W.C. Summers, D.L. Gilbert, R.S. Manalis, N.W.Daw, and R.J.Lasek. 1974. A guide to laboratory use of the squid *Loligo pealei*. Marine Biological Laboratory, Woods Hole, Mass. 74 p.

Bertin, J. 1981. Graphics and graphic information-Processing. Transl. by W. J Berg and P. Scott — Walter de Gruyter, New York. 273 p.

Burukovsky, R.N., Yu.M. Froerman, and Ch.M. Nigmatullin. 1984. Reproductive biology and scale of maturity stage of reproductive system of female squid (*Illex illecebrosus*). Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 84(IX/120): 4 p.

Caddy, J.F. 1983. The Cephalopods: Factors relevant to their population dynamics and to the assessment and management of stocks. *in* Advances in assessment of world cephalopod resources. Progrès réalises dans l'évaluation des ressources mondiales de céphalopodes. Progresos realizados en la evaluación mundial de cefalópodos. J. F. Caddy (ed.). FAO Fish. Tech. Pap./FAO, Doc. Tech. Pêches/FAO, Doc. Tec. Pesca 231: 416-452.

Coelho, M.L., H. Dupouy, and T. Amaratunga. 1982. Some histological observations on gonadal development of *Illex illecebrosus* (Le Sueur). Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 82(VI/30): 13 p.

Coelho, M.L., and R.K. O'Dor. 1984. Male sexual features of *Illex illecebrosus* and maturity staging. Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 84(IX/101): 22 p.

Dawe, E.G. 1981. Development of the Newfoundland squid (*Illex illecebrosus*) fishery and management of the resource. J. Shellfish Res. 1(1): 137-142.

Dawe, E. G., and P. C. Beck. 1985*a*. Distribution and size of short-finned squid (*Illex illecebrosus*) larvae in the northwest Atlantic from winter surveys in 1969, 1981, and 1982. J. Northwest Atl. Fish. Sci. 6(2): 43-45.

Dawe, E. G., and P. C. Beck. 1985*b*. Distribution and size of juvenile short-finned squid (*Illex illecebrosus*) (Mollusca: Cephalopoda) south of Newfoundland during winter. Vie et Milieu 35(3/4): 139-147.

Dawe, E.G., P.C. Beck, H.J. Drew, and G.H. Winters. 1981*a*. Long-distance migration of a short-finned squid (*Illex illecebrosus*). J. Northwest. Atl. Fish. Sci. 2: 75-76.

Dawe, E.G., and H.J. Drew. 1981. Historical records of mature female short-finned squid (*Illex illecebrosus*) from the northwest Atlantic and the first record of a mature female captured inshore at Newfoundland. J. Northwest Atl. Fish. Organ. Sci. 2: 61-65.

Dawe, E.G., G.R. Lilly, and H.J. Drew. 1983. Predation by short-finned squid (*Illex illecebrosus*) in Newfoundland inshore waters. Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 83(IX/74): 16 p.

Dawe, E.G, G.R. Lilly, and J.A. Moores. 1981*b*. An examination of the influence of squid (*Illex illecebrosus*) on recruitment in several finfish stocks off eastern Newfoundland and Labrador. Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 81(VI/25): 14 p.

Durward, R.D., T. Amaratunga, and R.K. O'Dor. 1979. Maturation index and fecundity for female squid, *Illex illecebrosus* (LeSueur, 1821). Int. Comm. Northwest Atl. Fish. Res. Bull. No. 14: 67-72.

Durward, R.D., E. Vessey, R.K. O'Dor, and T. Amaratunga. 1980. Reproduction in the squid, *Illex illecebrosus*: first observations in captivity and implications for the life cycle. Int. Comm. Northwest Atl. Fish. Sel. Pap. No. 6: 7-13.

Ennis, G.P., and P.W. Collins. 1979. Food and feeding of the short-finned squid, *Illex illecebrosus*, during its seasonal occurrence in the Newfoundland area. Int. Comm. Northwest Atl. Fish. Sel. Pap. No. 5: 25-29.

Fedulov, P.P., and Y.M. Froerman. 1980. Effect of abiotic factors on distribution of young shortfin squids, *Illex illecebrosus* (LeSueur, 1821). Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 80(VI/98): 22 p.

Froerman, Y.M. 1984. Feeding spectrum and trophic relationships of short-finned squid (*Illex illecebrosus*) in the Northwest Atlantic. Northwest Atl. Fish. Organ. Sci. Coun. Studies 7: 67-76.

Hamabe, M., C. Hamuro, and M. Ogura. 1982. Squid jigging from small boats. FAO Fishing Manuals. Fishing News Books Ltd. 74 p.

Hatanaka, H., S. Kawahara, Y. Uozumi, and S. Kasahara. 1985. Comparison of life cycles of five ommastrephid squids fished by Japan: *Todarodes pacificus, Illex illecebrosus, Illex argentinus, Nototodarus sloani sloani* and *Nototodarus sloani gouldi*. Northwest Atl. Fish. Organ. Sci. Coun. Studies 9: 59-68.

Hayashi, S. 1960. Development of the squid, *Ommastrephes sloani pacificus* (Steenstrup). Nagasaki Daigaku Suisangakubu Kenkyo Hokoku / Bull. Fac. Fish. Hagasaki Univ. 9: 43-48.

Hirtle, R.M.W., M.E. Demont and R.K. O'Dor. 1981. Feeding, growth and metabolic rates in captive short-finned squid, *Illex illecebrosus*, in relation to the natural population. J. Shellfish Res. 1(2): 187-192.

Hixon, R.F., R.T. Hanlon and W.H. Hulet. 1981. Growth and maximal size of the long-finned squid *Loligo pealei* in the northwestern Gulf of Mexico. J. Shellfish Res. 1(2): 181-185.

Hurley, G.V. 1980. Recent developments in the squid, *Illex illecebrosus*, fishery of Newfoundland, Canada. Mar. Fish. Rev. 42(7-8): 15-22.

Juanico, M. 1983. Squid maturity scales for population analysis. *in* Advances in assessment of world cephalopod resources. Progrès réalises dans l'évaluation des ressources mondiales de céphalopodes. Progresos realizados en la evaluación mundial de cefalópodos. J. F. Caddy (ed.). FAO Fish. Tech. Pap./FAO, Doc. Tech. Pêches/FAO, Doc. Tec. Pesca 231: 341-378.

Lange, A.M.T. 1980. The biology and population dynamics of the squids, *Loligo pealei* (LeSueur) and *Illex illecebrosus* (LeSueur), from the Northwest Atlantic. M.Sc. thesis, Univ. of Wash., Seattle Wash., 178 p.

Lange, A.M.T. 1984*a*. An assessment of the long-finned squid resource off the northeastern United States, autumn 1984. NMFS, NEFC, Woods Hole Lab. Ref. Doc. No. 84-37. 24 p.

Lange, A.M.T. 1984*b*. Status of the short-finned squid (*Illex illecebrosus*) off the northeastern U.S.A., November 1984. NMFS, NEFC, Woods Hole Lab. Ref. Doc. No. 84-38. 20 p.

Lange, A.M.T., and M.P. Sissenwine. 1983. Squid resources of the northwest Atlantic. *in* Advances in assessment of world cephalopod resources. Progrès réalises dans l'évaluation des ressources mondiales de céphalopodes. Progresos realizados en la evaluación mundial de cefalópodos. J. F. Caddy (ed.). FAO Fish. Tech. Pap./FAO, Doc. Tech. Pêches/FAO, Doc. Tec. Pesca 231: 21-54.

Lilly, G.R., and D.R. Osborne. 1984. Predation by Atlantic cod (*Gadus morhua*) on short-finned squid (*Illex illecebrosus*) off eastern Newfoundland and in the northeastern Gulf of St. Lawrence. Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 84 (IX/108): 16 p.

Lipinski, M. 1977. The place of squids in the biological and fishery structure of the world ocean. *in* Squid symposium. June 5-6. 1973, Gydnia. M. Lipinski (Ed.). Trans. from Polish. Foreign Scientific Publications Dept., Nat. Centre for Scientific, Technical and Economic Information. 173 p.

Maurer, R.O., and R.E. Bowman. 1985. Food consumption of squids (*Illex illecebrosus* and *Loligo pealei*) off the northeastern United States. Northwest Atl. Fish. Organ. Sci. Coun. Studies 9: 117-124.

Mercer, M.C. 1973*a*. Sexual maturity and sex ratios of the ommastrephid squid, *Illex illecebrosus*, at Newfoundland (Subarea 3). Int. Comm. Northwest Atl. Fish. Res. Doc. 73/71: 14 p.

Mercer, M.C. 1973*b*. Nominal catch of squid in Canadian Atlantic waters (Subareas 2-4), 1920 to 1968. Int. Comm. Northwest Atl. Fish. Res. Doc. 73/73: 10 p.

Mercer, M.C. 1975. Modified Leslie-Delury population models of the long-finned pilot whale (*Globicephala melaena*) and annual production of the short-finned squid (*Illex illecebrosus*) based upon their interaction at Newfoundland. J. Fish. Res. Bd. Can. 32(7): 1145-1154.

Mesnil, B. 1977. Growth and life cycle of squid, *Loligo pealei* and *Illex illecebrosus*, from the Northwest Atlantic. Int. Comm. Northwest Atl. Fish. Sel. Pap. No. 2: 55-69.

Mohn, R.K. 1981. Indices of abundance and bottom temperature relationships for squid in Div. 4VWX. Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 81(IX/99): 10 p.

Naef, A. 1923. Die cephalopoden. Fauna Flora Golfo Napoli Monographia, 35(1). plates 9-12.

O'Dor, R.K. 1983. *Illex illecebrosus. in* Cephalopod Life Cycles Vol. 1. P.R. Boyle (ed.). Academic Press 1983. p. 175-199.

O'Dor, R.K., and N. Balch. 1985. Properties of *Illex illecebrosus* egg masses potentially influencing larval oceanographic distribution. Northwest Atl. Fish. Organ. Sci. Coun. Studies 9: 69-76.

O'Dor, R.K., N. Balch, E.A. Foy, R.W.M. Hirtle, D.A. Johnston, and T. Amaratunga. 1982. Embryonic development of the squid, *Illex illecebrosus*, and effect of temperature on development rates. J. Northwest Atl. Fish. Sci. 3(1): 41-45.

O'Dor, R.K., R.D. Durward, E. Vessey, and T. Amaratunga. 1979. Feeding and growth rates in captive squid (*Illex illecebrosus*) and the influence of food availability on growth in the natural population. Int. Comm. Northwest Atl. Fish. Res. Doc. 79(II/16): 16 p.

O'Dor, R.K., E. Vessey, and T. Amaratunga. 1980. Factors affecting fecundity and larval distribution in the squid, *Illex illecebrosus*. Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 80(II/39): 9 p.

Roper, C.F.E., and C.C. Lu. 1978. Rhynchoteuthion larvae of Ommastrephid squids of the western North Atlantic, with the first description of larvae and juveniles of *Illex illecebrosus*. Proc. Biol. Soc. Wash. 91(4): 1039-1059.

Roper, C.F.E., C.C. Lu, and K. Mangold. 1969. A new species of *Illex* from the western Atlantic and distribution aspects of other *Illex* sp. (Cephalopoda: Oegopsida). Proc. Biol. Soc. Wash. 83: 295-322.

Roper, C.F.E., M.J. Sweeney and C.E. Nauen. 1984. FAO species catalogue. Vol. 3. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. FAO Fish. Synop., 125 Vol. 3: 277p.

Rowell, T.W. 1986. Management units and the squid resources of the Gulf of Maine, *Illex illecebrosus* and *Loligo pealei* . Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 86/59: 21 p.

Rowell, T.W., and R.W. Trites. 1985. Distribution of larval and juvenile *Illex* (Mollusca: Cephalopoda) in the Blake Plateau region (Northwest Atlantic). Vie et Milieu 35(3/4): 149-161.

Rowell, T.W., R.W. Trites, and E.G. Dawe. 1985*a*. Distribution of short-finned squid (*Illex illecebrosus*) larvae and juveniles in relation to the Gulf Stream frontal zone between Florida and Cape Hatteras. Northwest Atl. Fish. Organ. Sci. Coun. Studies 9: 77-92.

Rowell, T.W., J.H. Young, J.C. Poulard and J.P.Robin. 1985*b*. Changes in distribution and biological characteristics of *Illex illecebrosus* on the Scotian Shelf, 1980-83. Northwest Atl. Fish. Organ. Sci. Coun. Studies 9: 11-26.

Schuldt, M. 1979. Contribución al conocimiento del ciclo reproductor de *Illex argentinus*. Monogr. Commun. Invest. Cient., Argent. 10: 110 p.

Scott, J.S. 1978. Distribution of squid, *Illex illecebrosus*, on the Scotian Shelf 1970-76. Int. Comm. Northwest Atl. Fish. Sel. Pap. No. 3: 93-96.

Squires, H.J. 1957. Squid, *Illex illecebrosus* (LeSueur), in the Newfoundland fishing area. J. Fish. Res. Board Can. 14(5): 693-728.

Summers, W.C. 1971. The age and growth of *Loligo pealei*, a population study of the common Atlantic Coast squid. Biol. Bull. (Woods Hole). 141: 189-201.

Trites, R.W., and T.W. Rowell. 1985. Larval and juvenile distribution of the short-finned squid (*Illex illecebrosus*) in the Cape Hatteras-Florida Straits area in the December-January period, 1984-1985. Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 85(VI/69): 36 p.

Vecchione, M. 1978. Larval development of *Illex* (Steenstrup, 1880), in the northwestern Atlantic, with comments on *Illex* larval distribution. Proc. Biol. Soc. Wash. 91(4): 1060-1075.

Vinogradov, V.I. 1984. On feeding of two squid species in the northwest Atlantic. Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 84(IX/117): 7 p.

Voss, G.L. 1956. A review of the cephalopods of the Gulf of Mexico. Bull. Mar. Sci. Gulf Caribb. 6: 85-178.

Voss, G.L. 1983. A review of cephalopod fisheries biology. Memoirs of the National Museum Victoria, 44: 229-241.

Voss, G.L., and T.F. Brakoniecki. 1985. Squid resources of the Gulf of Mexico and southeast Atlantic coasts of the United States. Northwest Atl. Fish. Organ. Sci. Coun. Studies 9: 27-38.

Vovk, A.N. 1974. The position of the longfin squid *Loligo pealei* (LeSueur) in the ecosystem. Tr. Atl. Nanchno Issled. Inst. Ryb. Khoz. Okeanogr. 58168-:176. English trans. Fish. Mar. Ser. Trans. ser. No. 3977.

Vovk, A.N. 1983. Food relations of long-finned squid, *Loligo pealei* (LeSueur), in the Northwest Atlantic and its position in the ecosystem. Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 83(IX/83): 20 p.

Waldron, D.E. 1983. Factors influencing Scotian Shelf finfish and squid interactions with special reference to silver hake. Northwest Atl. Fish. Organ. Sci. Coun. Res. Doc. 83(IX/92): 28 p.

Wallace, I.C., R.K. O'Dor, and T. Amaratunga. 1981. Sequential observations on the digestive process in the squid, *Illex illecebrosus*. Northwest Atl. Fish. Organ. Sci. Coun. Studies 1: 65-69.

Webber, D.M. and R.K. O'Dor. 1985. Respiration and swimming performance of short-finned squid (*Illex illecebrosus*). Northwest Atl. Fish. Organ. Sci. Coun. Studies 9: 133-138.

Whitaker, J.D. 1980. Squid catches resulting from trawl surveys off the southeastern United States. Mar. Fish. Rev. 42 (7-8): 39-43.

Wiseman, E. 1982. Annex to the Worldwide Fisheries Marketing Study. Prospects to 1985. Dept. of Fish. and Oceans Fish. Econ. Devel. & Mark. Rep.: 109 p.

Worms, J. 1983. World fisheries for Cephalopods: a synoptic overview. *in* Advances in assessment of world cephalopod resources. Progrès réalises dans l'évaluation des ressources mondiales de céphalopodes. Progresos realizados en la evaluación mundial de cefalópodos. J. F. Caddy (ed.). FAO Fish. Tech. Pap./FAO, Doc. Tech. Pêches/FAO, Doc. Tec. Pesca 231: 1-20.